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ABSTRACT

Kenneth Miles Leber. SEASONAL COMMUNITY DYNAMICS OF MACROBENTHOS ON A HIGH ENERGY SANDY BEACH IN NORTH CAROLINA. (Under the direction of Edward P. Ryan) Department of Biology, August, 1977.

Twelve macrobenthic species representing three phyla--Arthropoda, Mollusca, and Annelida--were taken during bi-monthly day and night sampling of a high energy sandy beach on Bogue Banks, North Carolina. Core tubes, sieves, seine, and dip nets employed over a 15 month period provided data indicating strong interaction among species of the three beach habitats--upper beach, intertidal, and nearshore surf zones. These regions were highly inter-related through trophi-dynamics and overlapping spatial requirements of the composite species; these factors contribute to the pulse stability of the community evident on the beach.

The five most dominant species ranked according to relative abundance and frequency were Emerita talpoida, Donax variabilis, Donax parvula, Arenaeus cribrarius, and Ocypode albicans. Length frequency polygons determined for these species indicated that growth and recruitment were seasonally regulated. Standing crop was estimated at over 2,400 g ash-free dry weight. m^{-1} beach frontage in

September 1976. A qualitative trophic model was constructed and indicated that Emerita and Donax are important to the system as energy converters. Fish and crabs, especially Ocypode and Arenaeus, migrated nightly, and birds daily, to feed in the intertidal zone except during colder months.

Variations in tidal migratory activity were observed for E. talpoida, D. variabilis, and D. parvula (a species whose life history has not been adequately described). These species typically migrated up and down the beach in the wash zone. In mid August 1976, Donax populations stopped migrating; D. variabilis remained stranded high on the beach during ebbing tides while D. parvula moved out of the wash zone into nearshore waters. This pattern was maintained during the remainder of 1976. Stranding of E. talpoida during ebbing tides began in September 1976 and became increasingly more common thru December 1976. In January 1977, both E. talpoida and D. variabilis moved offshore.

Seasonal variations of diversity were related to numerical dominance by Emerita. The Shannon-Weaver index declined from 1.05, typical during winter, spring, and early summer months, to 0.46 in late summer.

SEASONAL COMMUNITY DYNAMICS
OF MACROBENTHOS ON A HIGH ENERGY SANDY BEACH
IN NORTH CAROLINA

A Thesis
Presented to
the Faculty of the Department of Biology
East Carolina University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science in Biology

by
Kenneth Miles Leber
August 1977

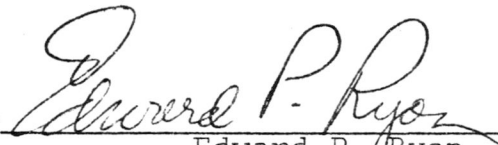
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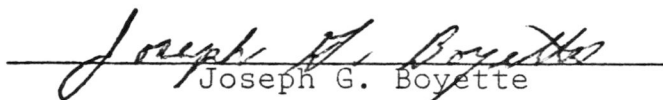
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INTRODUCTION

Community ecology on sandy beaches has been studied in terms of species assemblages (Pearse, Humm, and Wharton, 1942; Johnson, 1970; Dexter, 1969, 1974, 1976) and intertidal zonation (Dahl, 1953; Gauld and Buchanan, 1956; Rodriguez, 1959; Wade, 1967; Patterson, 1974). An appreciation of trophic interactions and seasonal changes within the beach ecosystem is essential to understanding community dynamics and stability. With the exception of the construction of a food web by Koepcke and Koepcke (1952), these topics have largely been neglected and few attempts have been made to define sandy beach systems in functional terms. In this study, seasonal community dynamics of macrobenthos on an Atlantic sandy beach are presented.

Presumably, the sandy beach community is interrelated with the adjacent ocean. Thus, community boundaries may overlap; the significance of this is not fully understood. Mills (1969) presents a comprehensive review of the history and controversy behind the ecological community concept including a discussion of marine benthic communities. The classification of these communities has led to insoluble confusion. The implication is that benthic marine communities intergrade into one another to such a

degree that it is difficult to define individual communities.

The sandy beach intertidal zone is particularly well suited as a location for studying this concept. It is a harsh habitat subject to widely fluctuating physical conditions and is less favorable for life than any other type of ocean shore except gravel or cobble beaches (Hedgpeth, 1957). Thus, it would seem likely that this environment could support a discrete community of organisms specifically adapted to physical stresses which would present barriers to species from adjacent communities.

A knowledge of life histories of organisms within this ecosystem is important in terms of describing community boundaries and structure. While population studies are available for particular beach organisms (Pearse et al., 1942 and Diaz, 1974 for Emerita talpoida; Cowles, 1908 and Haley, 1969 for Ocypode albicans; Loesch, 1957 and Edgren, 1959 for Donax variabilis; and Wade, 1967 for Donax denticulatus), other species have been neglected, especially the beach clam, Donax parvula, and Arenaeus cribrarius, a portunid crab.

Thus the objectives of this study are to: (1) define the structure of the macrobenthic community on a North Carolina sandy beach in terms of species rank, relative abundance, seasonal succession, and stratification,

(2) describe seasonal changes in dominance and diversity, (3) compose a qualitative trophic model for this sandy beach, (4) examine pertinent population dynamics in dominant and sub-dominant fauna (dominance determined by ranked importance values), and (5) describe macrobenthic species interactions and relate them to community stability and the degree to which the beach community is functionally discrete from adjacent systems. These data from a temperate sandy beach may add to our understanding of marine benthic communities.

METHODS AND STUDY SITE

Description of Study Site

This study was conducted on Bogue Banks, one of the southernmost barrier islands in North Carolina (Figure 1). The site was centered about 30 km west of Morehead City, 1.5 km east of Bogue Pier, and encompassed 1 km along the shore of this south facing high energy beach. Odum, Copeland, and McMahan (1974) describe high energy beaches as sandy shores which receive strong wave action. Waves on Bogue Banks averaged 0.5 to 1.0 m from crest to trough during this study. The major limiting factor that this site imposes upon organisms is substrate instability due to wave action.

The beach is flanked on the landward side by an accretionary sand dune 3 to 4 m high. The dune is stabilized by several plants including sea oats, Uniola paniculata; American beachgrass, Ammophila breviligulata; seacoast blue-stem, Andropogon littoralis; bitter panicum, Panicum amarum; and seaside goldenrod, Solidago sempervirens. A succulent plant, sea rocket, Cakile edentula, grows at the seaward base of the dune and down onto the beach.

A short distance inland from the foredune lies a maritime forest which has been cut through at roughly 100 m intervals. Paved roads have been constructed in these

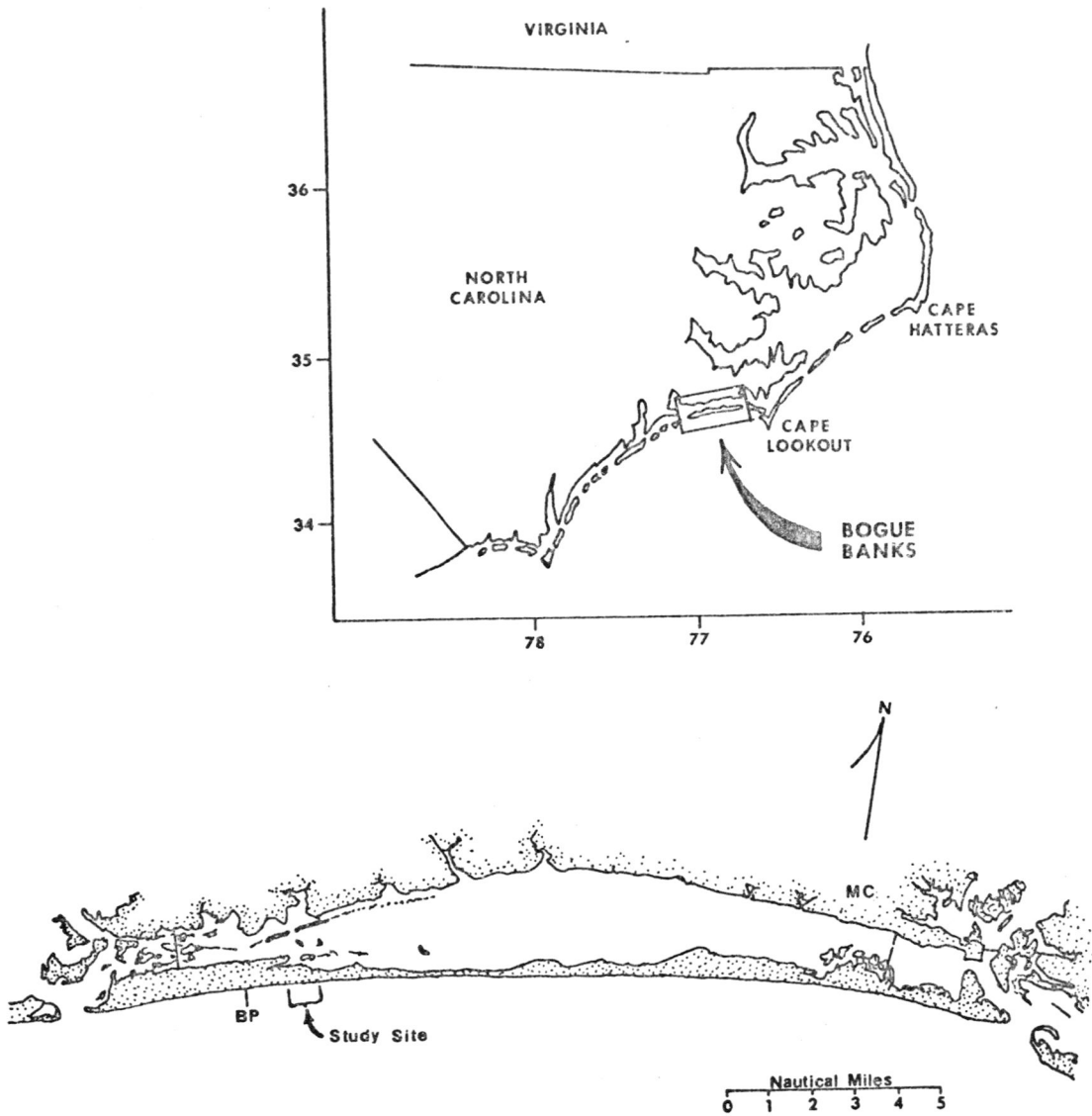


Figure 1. The study site on Bogue Banks, North Carolina. Insert gives position relative to other N.C. outer banks.

BP - Bogue Pier
 MC - Morehead City

cuts from the coast highway (route 58) to a road running parallel to the foredune. The number of dwellings in this area has increased from one in January 1976 to 12 in April 1977.

Width of the beach from the foredune base to spring tide high water mark is about 15 m. The low tide terrace adds an additional 40 m to beach width during low spring tides. The beach slope ratio, measured from the foredune base to the high tide mark, is 11:1. Semi-diurnal tidal fluctuations vary from 0.7 m to 1.25 m (NOAA, 1975). The beach is composed of quartz sand.

Bogue Banks is historically a relatively stable area except near its bordering inlets (Pilkey, Pilkey, and Turner, 1975). The island is subject to overwash (Fisher, 1967) but it is more stable than N.C. barrier islands with north-south axes. On a long term basis, north-south barrier islands have been eroding while east-west barrier islands have been accreting. One theory for this is the Cape Shoal Process which maintains that during large storms shoal sediment which has built up off the tips of barrier island capes "...is shifted westward into the east-west system where it migrates onshore during more normal lower energy conditions as a 'slug' of sediment. Shore processes eventually build this slug into a new dune ridge system" (Riggs and Benton, 1977).

Zonation

There are at least four distinct zones on this sandy beach (Figure 2). Modified after Wade's (1967) scheme in which there was no damp zone, these areas conform to the following classification:

Spray Zone

This is the dry upper beach which lies above spring tide high water levels and is commonly subject to salt spray and wind blown sands.

Damp Zone

A subdivision of the broader intertidal zone, the damp zone is the area left exposed on an ebbing tide. At its uppermost boundary lies the drift line which is deposited at high tide and consists of accumulated plant and animal debris.

Wash Zone

This area is covered intermittently by the uprush of water following each incoming wave, and migrates up and down the beach obscuring the damp zone at high tide. It is further divided into two subzones: the saturated zone which is characterized by a continual slick of water on its surface, and the wet zone which is characterized by drainage between successive uprushes and frequently

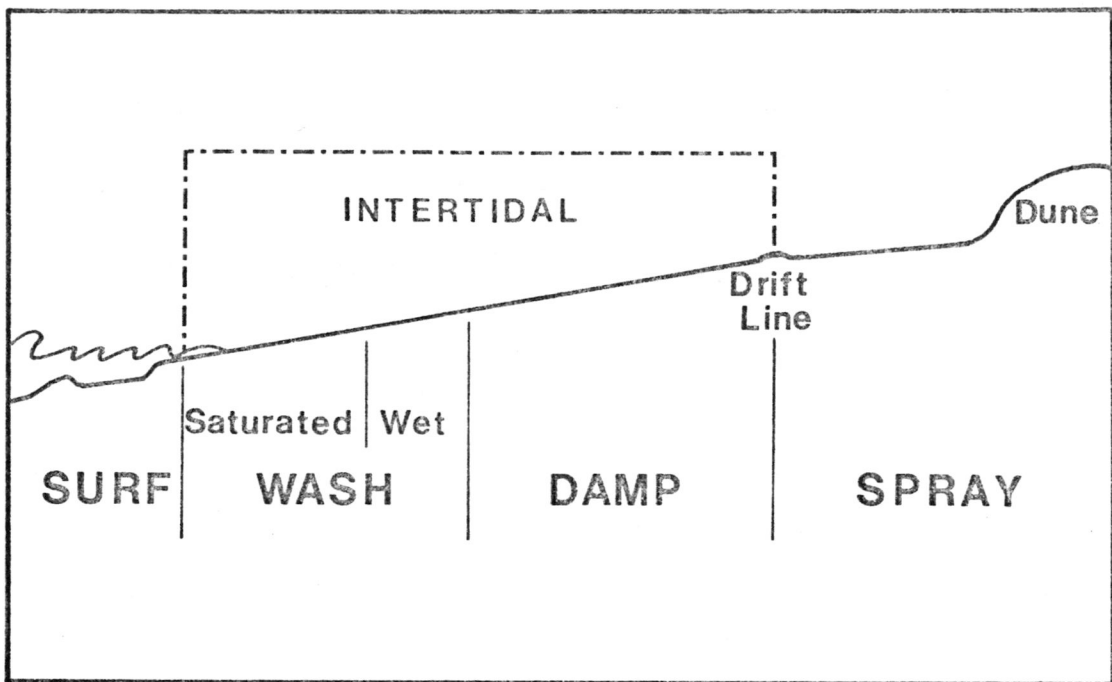


Figure 2. Profile of study area indicating zonation on beach (Modified after Wade, 1967).

periodic wetting by larger waves. The wash zone is located within the confines of the broader intertidal zone which is defined as the region between mean high and mean low tides.

Surf Zone

This area is covered by shallow water and is subject to strong currents and pounding surf.

Field Work

Macrobenthic organisms were collected bimonthly from December 1975 through April 1977. Both day and night samples were taken on each collection date. Sampling was directed towards the intertidal and nearshore surf zones. Mid season diurnal sampling was performed in July and October of 1976, and in February of 1977.

Physical Measurements

During each sampling effort air and water temperatures were taken with a centigrade thermometer while salinity was determined with a Goldberg temperature compensated refractometer (American Optical model no. 10419) calibrated in parts per thousand ($\pm 0.1\%$ error). Substrate temperatures were taken from October 1976 through April 1977 with a Yellow Springs thermistor and a 90 cm probe. During the fall and winter diurnals, temperature readings

were recorded at regular time intervals for air, water, sand surface, 2 cm, 10 cm, and 70 cm depths on the upper beach.

Sampling

A hand held sieve scoop for collecting organisms was constructed by attaching a wooden pole to a metal frame with an aluminum digging edge 59 cm long, over which was stretched 3 mm mesh hardware cloth. A 1.0 mm mesh removable outer liner was attached. One half meter square scoops were taken in the high, mid, and low wash zone with replicates every 25 m over 100 m of beach frontage. The scoop was employed by raking in the substrate to a depth of about 5 cm, allowing the backwash of a wave to filter sand through the sieve. Scoop sample collections were made during mid tide, as determined from tide tables (NOAA, 1975).

Scoop samples were supplemented with core sampling in order to collect organisms burrowed deeper than the 5 cm depth sampled by the scoop. A core tube of 5 cm diameter was used to a depth of 15 cm during periods of higher densities (June through December). During other months a core tube of 13 cm diameter was utilized. Randomly located transects were set up during mid to low tides from high tide mark to surf zone. Five replicates spaced 1 m apart,

and perpendicular to the transect axis, were taken at 2 m intervals along each transect. Samples were sieved in a 1.0 mm mesh screen sieve box.

In order to sample organisms active on the beach only after dark, nocturnal collections were made along two transects running parallel to the water line for 1 km along the beach. One transect was located low in the intertidal zone in water about 0.25 m deep; the other was located along the wet line at the top of the wash zone. These transects were walked simultaneously by two persons beginning an hour after dark on a mid to high tide. Aided by a battery powered fluorescent light, the person in the water walked the transect recording densities with hand counters and taking mobile macrobenthic species in a small mesh dip net. Likewise, the person walking the wet line transect collected organisms and recorded densities. Species taken during day sampling were not collected at night. In order not to disturb the more rapidly moving organisms being counted along the wet line, species were taken with hand nets during warmer months only after counting and while walking back along the transect towards the starting point. All specimens collected during each sample date were placed in labeled jars, preserved with a mixture of 70% ethanol, 28% water, and 2% glycerin, for laboratory analysis.

During diurnals, previously established sample methods were repeated at 3 h intervals over a 24 h period. In addition, gut contents of fish, collected in the wash zone with a 50 ft bag seine and a dipnet, were examined for macrobenthos at this time.

In early December 1976, plaster molds of Ocypode burrows were made in order to determine depths of burrows prior to winter dormancy. Plaster of Paris was mixed with water to a semi-fluid consistency and poured into burrows. After hardening, the casts were excavated using a shovel.

Laboratory Work

Identifications

Most identifications were made with the aid of general taxonomic references (Miner, 1950; Pettibone, 1963; Williams, 1965; Gosner, 1971; and Bousfield, 1973). Hugh Porter of the University of North Carolina Institute of Marine Sciences in Morehead City, N.C. assisted in the identification of bivalves.

Preserved specimens in each sample jar were counted, sexed, and carapace dimensions were measured to 0.1 mm. For sample dates in which over 100 individuals of a species were collected, approximately 100 were obtained for sexing and measuring by randomly subsampling each nth individual during the initial counting (n was determined by dividing

the estimated total number of organisms by 100).

Determination of sex in Emerita was established in accordance with Snodgrass (1952). Males were identified by the absence of pleopods on abdominal segments and by the presence of thick, soft papillae (through which open the genital exit ducts) on the coxopodites of the fifth legs. Females were identified by the presence of pleopods on various abdominal segments and the oviduct openings on the coxae of the third legs. Sex was not ascertained for Donax.

Data Analysis and Experimentation

Ash free dry weights (AFDW) were determined for the five most abundant and frequently collected species as follows. Selected members from each size class were dried in a drying oven at 88°C, weighed, ashed in a muffle furnace at 520°C and reweighed. Prior to ashing decapod crustacea, a ground subsample was decalcified with dilute HCl until effervescence completely ceased in order to eliminate inorganic carbon loss during ashing due to partial volatilization of CO₂ from CaCO₃ in the exoskeleton. This mixture was then dried, reweighed and ashed.

To predict AFDW of organisms without having to repeat the time consuming weighing and ashing procedure, regressions of log₁₀ AFDW on log₁₀ size were calculated and

expressed in the following form for predicting weight (Holme and McIntyre, 1971):

$$W = aL^b$$

or

$$\log_{10} W = a + b \log_{10} L$$

where 'W' is AFDW, 'L' the length of the animal; 'a' is a constant, the y-intercept, and 'b' the slope. A Fortran program incorporating the regression and size data was utilized to predict AFDW values with a Burroughs B5500 computer. An SPSS codebook program (Nie et al., 1975) was used to determine size class frequencies of certain species collected for each sample date (those species which were determined to be the five most dominant).

A short term experiment was carried out for testing the role of temperature in overwintering dormancy exhibited by Ocypode. Critical temperatures from this experiment were compared with field temperatures at the time when burrow activity ceased in the fall and began in the spring. Crabs taken in mid April 1977 were placed in jars of moist sand in a Shearer-Gillette (model no. CEL-37) plant growth chamber as soon as possible after collection. Temperatures were set to approximate environmental temperatures at the time of capture. After an acclimation period of 1 day, temperatures were gradually lowered (2°C per day)

until crabs entered a state of dormancy. Following several days in this dormant state, the crabs were subjected to gradually increased temperatures (2°C per day) with periodic observation for signs of activity. Active crabs constructed and crawled out of burrows periodically, while dormant crabs remained inactive in their burrows.

Densities and biomass of macrobenthos in this study are expressed as units of beach frontage. Area squared units are unsuitable in a region in which boundary limits are constantly changing with tidal fluctuations. For example, the wash zone, which supports vast herds of Emerita in late summer, may vary in width from 2 m at high tide to 12 or 15 m at low tide, depending upon the slope of the beach and location of the migrating wash zone.

RESULTS

Hydrographic Observations

Nearshore salinities were typically lower in winter months than in spring and summer months (Figure 3).

Salinities ranged from 33 to 36 parts per thousand.

Seasonal variations in air and water temperatures were distinct (Figure 3). Water temperatures ranged from 5 to 28°C while air temperatures ranged from 2 to 38°C. Fall temperatures in 1976 were characterized by a steep decline. Water temperature dropped to a low of 5°C in January 1977, compared to 10°C in January 1976.

Substrate temperatures taken on the high beach from late October 1976 to mid April 1977 are given in Figure 4. Temperature fluctuations were moderate at a depth of 70 cm, while variability at other levels was marked.

Diurnal substrate temperatures on the high beach showed a marked gradient evident throughout a 24 h period with distinct moderation at 70 cm depths (Figure 5). Temperatures taken during a warm, winter diurnal (26 February 1977) displayed a 24 h gradient, when graphed, similar to that of diurnal temperatures taken in early fall (23 October 1976), except at 70 cm depths. Temperatures at 70 cm depths were not affected by short term (diurnal) air temperature variation.

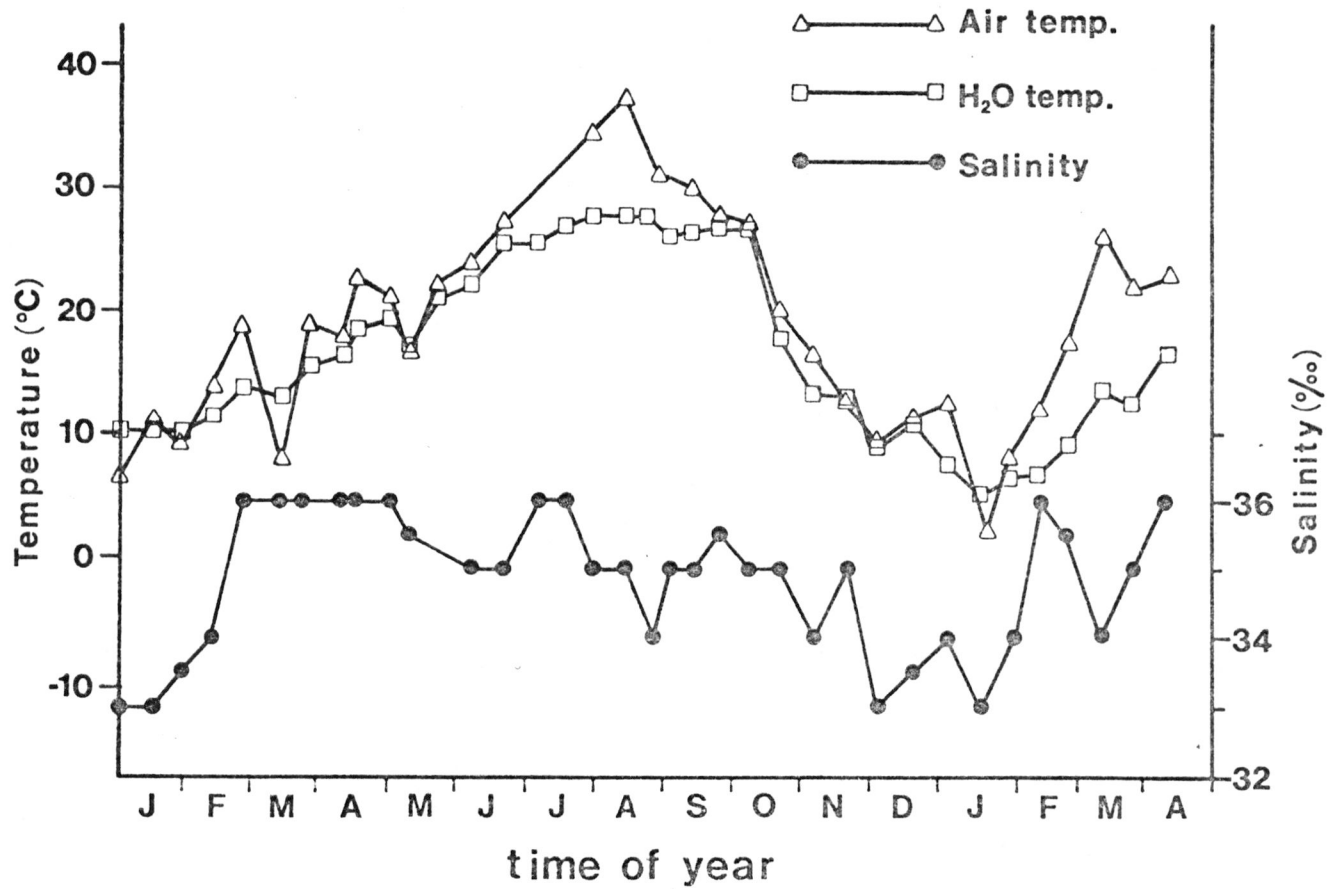


Figure 3. Comparisons of air, water, and salinity data showing relationship to time of year.

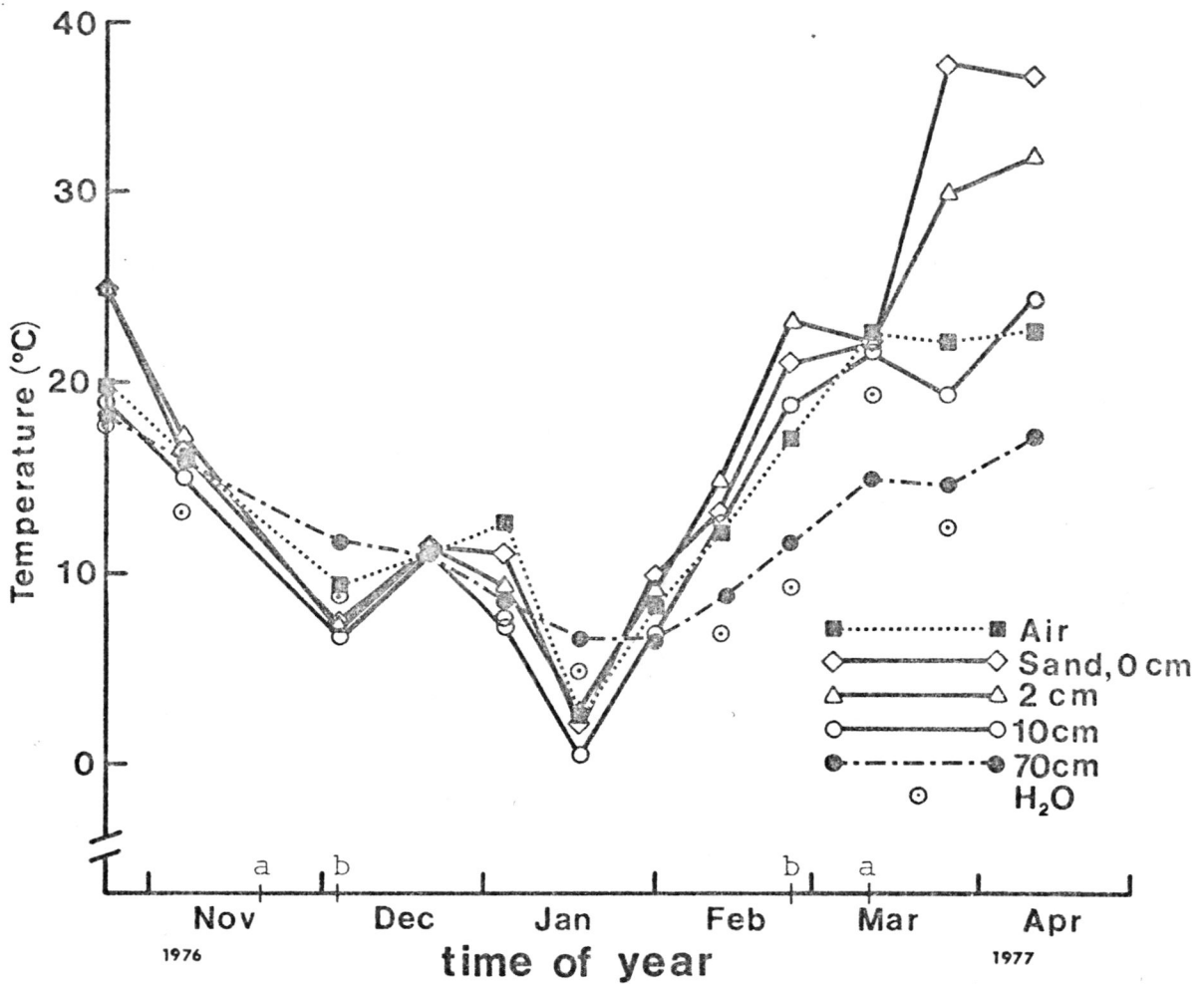


Figure 4. Air, substrate and water temperatures taken during fall, winter and spring of 1976-1977. All substrate temperatures were taken in the spray zone with a 90 cm thermistor probe.

- a. Ocypode burrow activity evident.
- b. Ocypode burrow activity not evident.

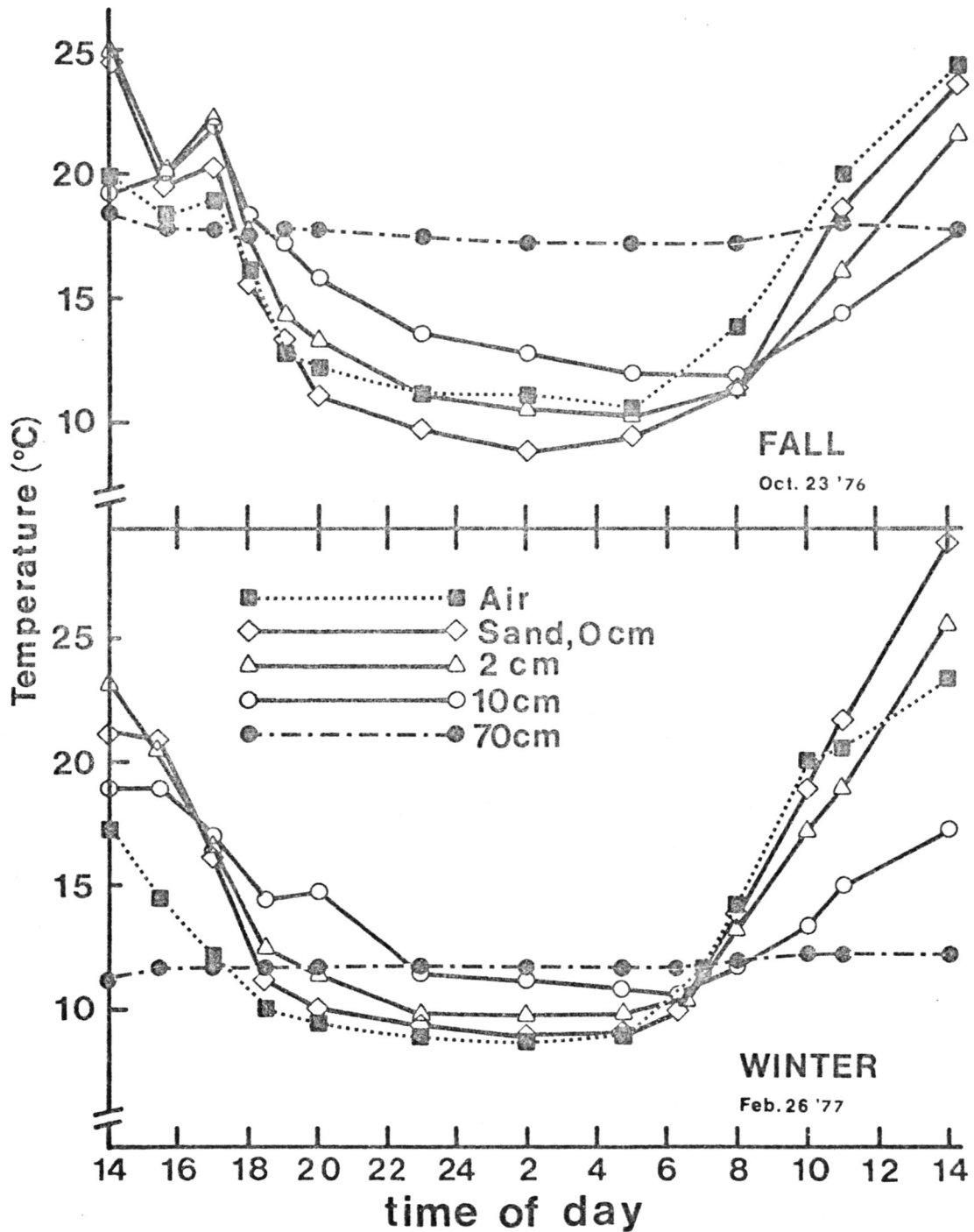


Figure 5. Comparison of 24-h air and substrate temperatures recorded in the spray zone during fall 1976 and winter 1977 diurnals.

Biotic Composition

Twelve species of macrobenthic organisms comprising three phyla - Arthropoda, Mollusca, and Annelida - were taken during this study (Table 1). Endemic species of both northern and southern latitudes were collected. Those species better adapted for northern climates included talitrid and haustoriid amphipods, Talorchestia megalopthalma, Haustorius canadensis, and Amphiporeia virginiana; the portunid crab, Ovalipes ocellatus; and the polychaete, Nephtys picta (Miner, 1950; and Williams, 1965). Ocypode albicans is typically a southern species (Dahl, 1953). Cape Hatteras, N.C. is about the northern limit of the range of both Donax variabilis and Donax parvula (Morrison, 1971). Morrison points out that virtually all Donax studies in the Carolina region have considered both of these species as one, D. variabilis, thus completely confusing growth studies of the two species. (Morrison, 1971, advocates renaming D. variabilis, using the specific name coined in 1849, D. roemeri protracta, while Porter (1974) suggests retaining the familiar D. variabilis).

The remaining decapods, Arenaeus cribrarius, Callinectes sapidus, and Emerita talpoida and the isopod, Chiridotea caeca, are common along the East Coast of the United States (Miner, 1950; Williams, 1965). It is significant

Table 1. Macrobenthic organisms collected during this study ranked by importance value^a, relative abundance, and relative frequency.

Importance Value Rank	Species	Importance Value	Rel Abun	Rank	Rel Freq	Rank
1	<i>Emerita talpoida</i> ^b	.350	.534	1	.166	2
2	<i>Donax variabilis</i> ^c	.203	.235	2	.172	1
3	<i>Donax parvula</i> ^c	.145	.207	3	.083	6
4	<i>Arenaeus cribrarius</i> ^b	.059	10 ⁻⁶	9	.118	3
5	<i>Ocypode albicans</i> ^c	.050	10 ⁻⁵	8	.101	4
6	<i>Amphiporeia virginiana</i> ^d	.047	.005	6	.088	5
7	<i>Haustorius canadensis</i> ^d	.046	.011	4	.083	7
8	<i>Talorchestia megalopthalma</i> ^d	.042	.001	7	.082	8
9	<i>Nephtys picta</i> ^d	.027	.007	5	.047	9
10	<i>Ovalipes ocellatus</i> ^d	.018	10 ⁻⁶	10	.036	10
11	<i>Callinectes sapidus</i> ^b	.009	10 ⁻⁸	11	.018	11
12	<i>Chirodotea caeca</i> ^b	.003	10 ⁻⁸	12	.006	12

a Relative abundance plus relative frequency \div 2.

b Ubiquitous along East Coast of U.S.A.

c Southern type locale.

d Northern type locale.

that all benthic species collected are capable of burrowing into the substrate.

Species are ranked in Table 1 in terms of importance values. Importance value calculations were determined for each species by dividing percent relative abundance plus percent relative frequency by two. Dominant species by importance values included the wash zone organisms E. talpoida, D. variabilis, and D. parvula.

Frequency and Relative Abundance

Seasonal fluctuations in species occurrence and relative abundance were distinct (Figure 6). H. canadensis and A. virginiana prevailed during winter months, while E. talpoida and D. variabilis dominated the beach during other seasons. D. parvula were abundant on the beach until August 1976, but were not observed in intertidal collections from mid August 1976 through mid February 1977. The large benthic predators, O. albicans and A. cribrarius, appeared on the beach only during warmer months (March to November). O. ocellatus first appeared in April and were collected in night samples until the end of July. Talitrids appeared intermittently throughout the year.

Numbers of individuals per unit length of beach are shown graphed against time of year in Figures 7 and 9. These data represent those individuals found in the tidal

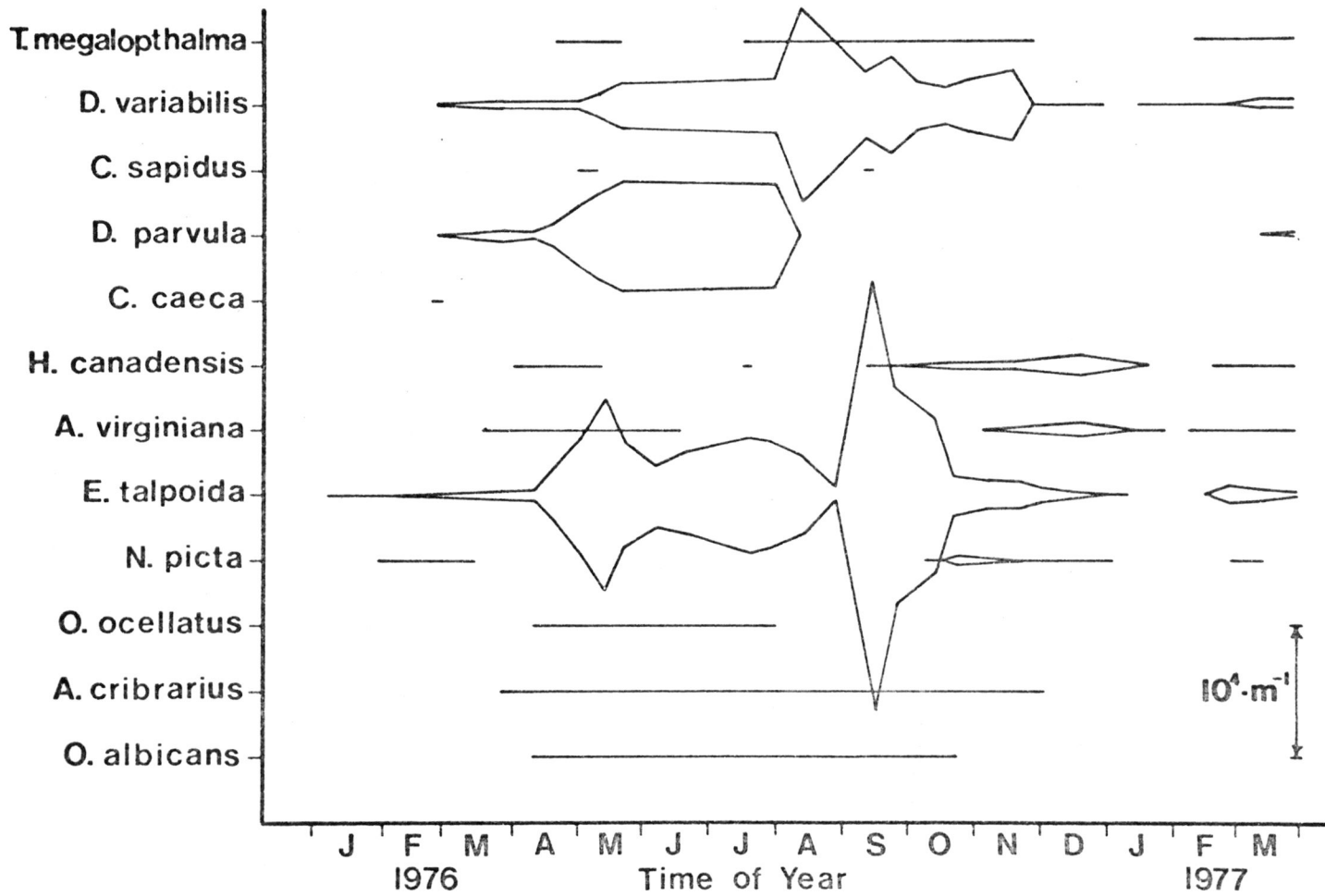


Figure 6. Seasonal fluctuations in species occurrence and relative abundance.

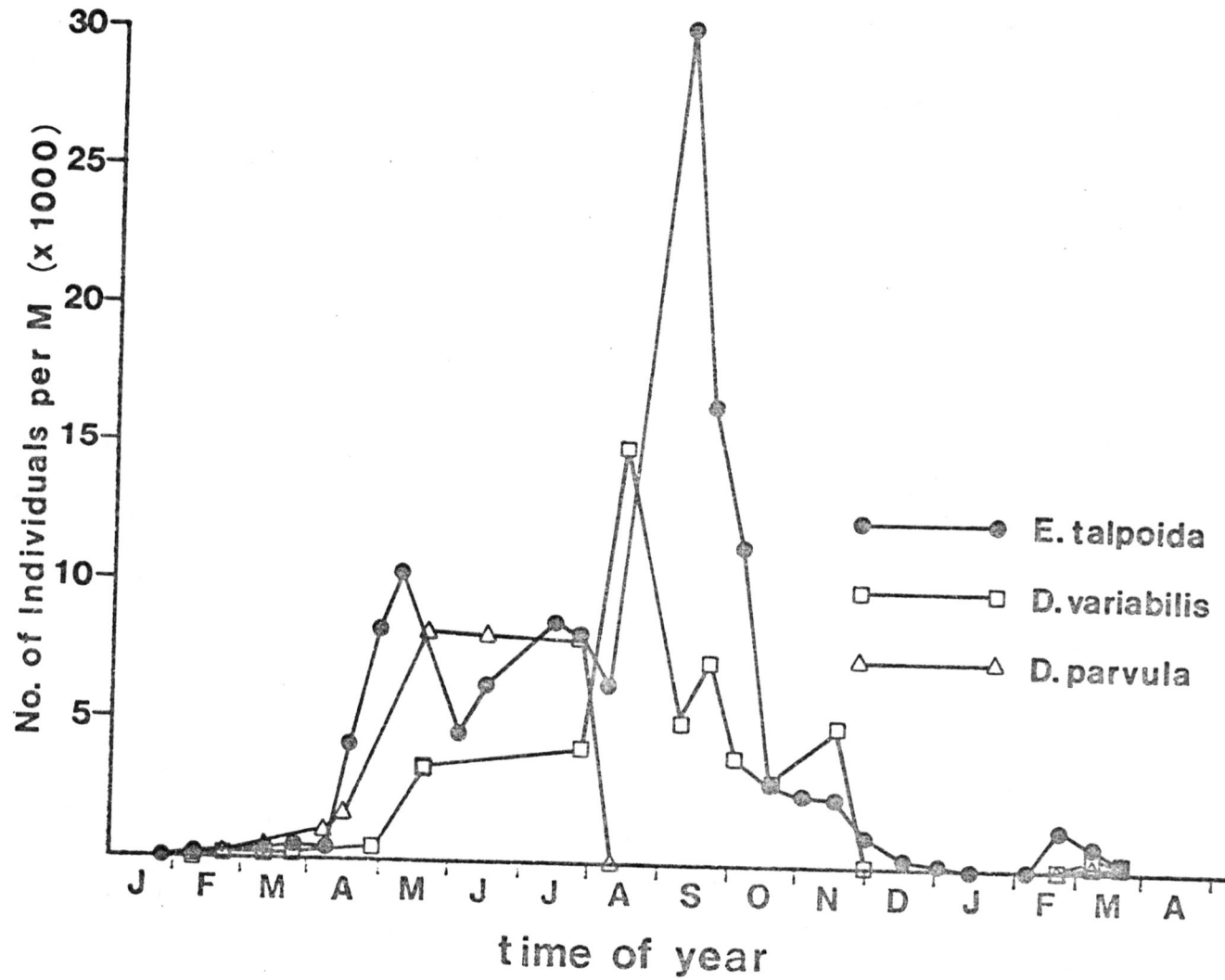


Figure 7. Densities of *Emerita* and *Donax* taken during this study.

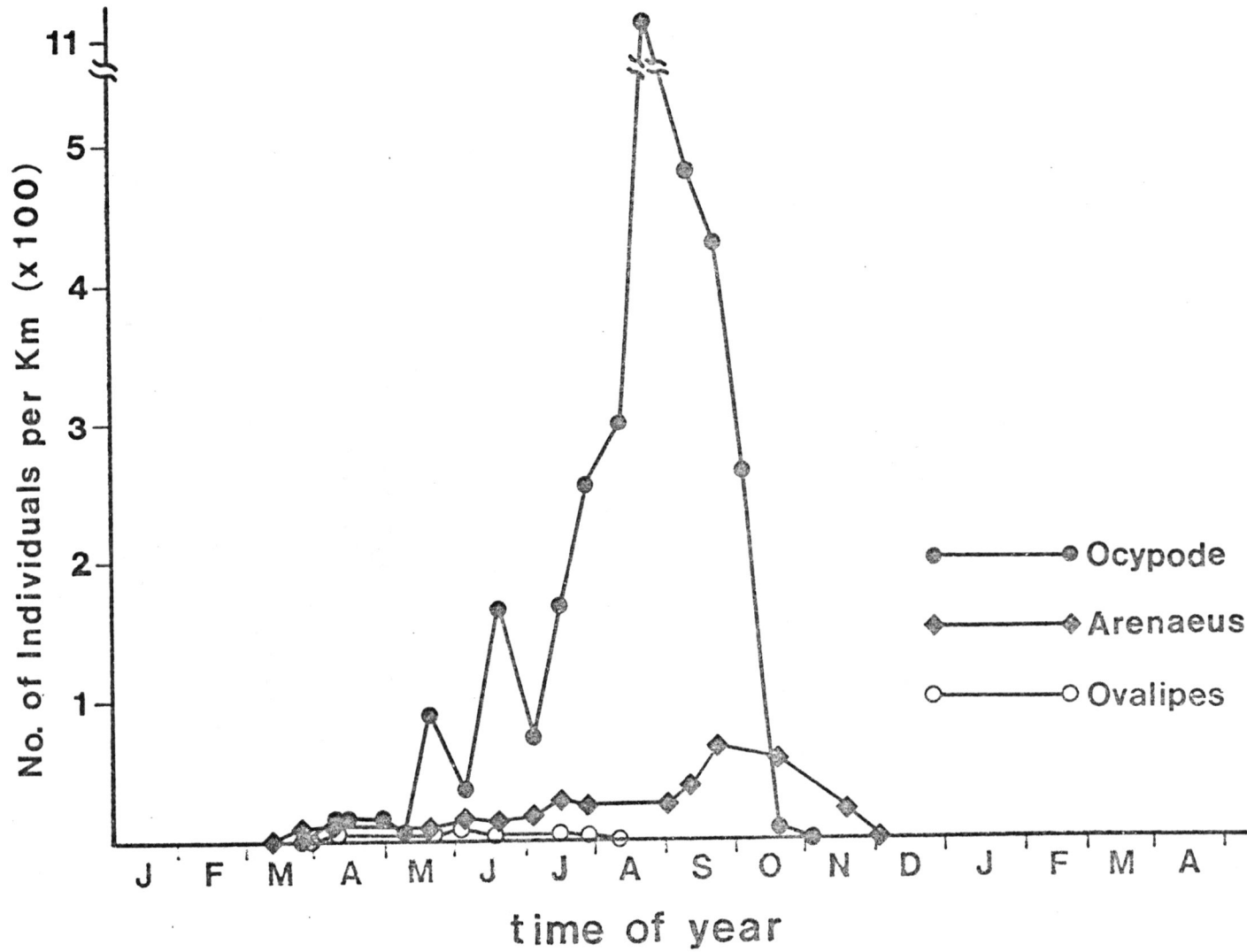


Figure 8. Densities of brachyuran crabs taken during this study.

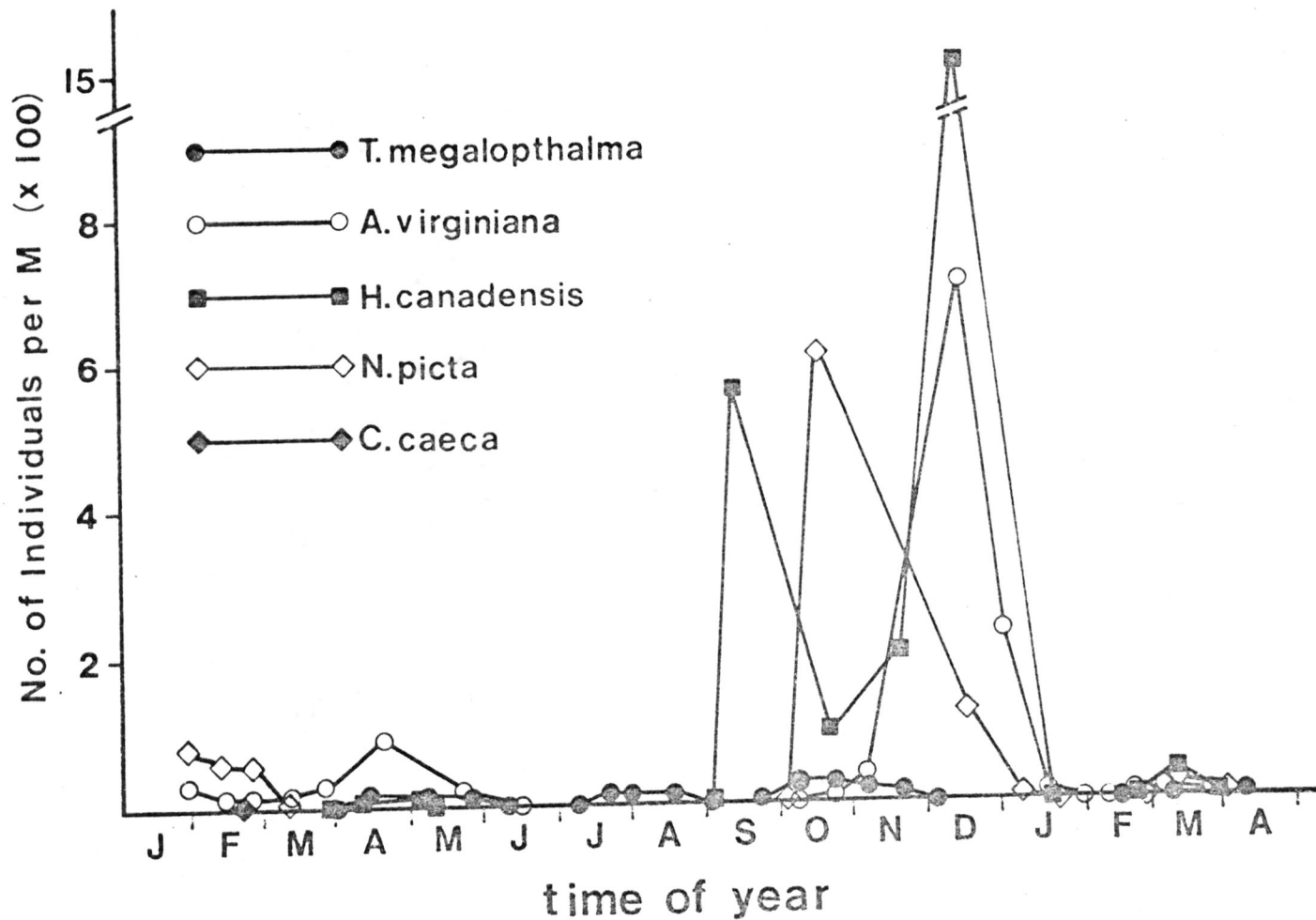


Figure 9. Densities of amphipods, isopods, and polychaetes taken during this study.

and nearshore surf zones. During periods of peak abundance in late summer, densities of Emerita and Donax (Figure 7) were typically four orders of magnitude greater than densities of other species (Figures 8 and 9).

Ocypode densities remained an order of magnitude higher than those of Arenaeus until mid October 1976 (Figure 8). From October 1976 through April 1977, ghost crabs remained in burrows.

Activity in Ocypode appeared to depend directly upon the minimum temperature range 12 to 15°C. Data is presented in Table 2 for the temperature tolerance experiment. Critical temperatures in the laboratory compare well with 70 cm depth field temperatures (Figure 4) taken at the time when burrow activity ceased in late November 1976, and subsequently began in early March 1977 following a period of winter dormancy.

Vertical Distribution and Migration

Vertical ranges of zonation varied considerably both among and within certain species (Figure 10). Ocypode utilized the spray zone as a shelter, but fed over the entire beach, especially in the wash zone during warmer months. The drift line supported at least one talitrid amphipod, the beach flea, T. megalopthalma. The polychaete, N. picta, and the isopod, C. caeca, were found in

Table 2. Temperature and burrow activity data from the Ocypode laboratory experiment.

Days in Chamber	Time of Observation	Temp(°C) in Chamber	Number in Burrows (non-plugged)	Number Outside Burrows	Number in Plugged Burrows
10 a	1300	16.5	6	12	0
10 b	2130	16.0	4	14	0
11 a	1000	16.0	5	13	0
11 b	1930	15.0	3	15	0
12 a	1400	16.0	5	13	0
12 b	2010	14.5	4	14	0
13 a	1515	14.5	5	13	0
13 b	2235	13.0	5	13	0
14 a	0900	14.0	6	12	0
14 b	1915	12.0 ^c	12	6	0
15 a	1100	12.0	11	7	0
15 b	2200	10.5	14	4	0
16 a	1630	11.5	10	8	0
16 b	2000	10.0	12	6	0
17 a	0945	10.5	10	7	1
17 b	2230	9.5	14	3	1
18 a	1600	9.0	16	0	2
18 b	2200	7.5	15	1	2
19 a	1000	7.5	16	0	2
19 b	1900	6.0	16	0	2
20 a	1600	9.5	15	1	2
20 b	2230	7.5	15	1	2
21 a	1000	11.0	14	2	2
21 b	1900	9.5	14	2	2
22 a	1100	13.0	13	3	2
22 b	2000	16.5	12	4	2
23 a	1200	15.0 ^d	7	9	2
23 b	2300	13.5	7	9	2
24 a	1000	16.0	4	12	2
24 b	2100	14.5	2	14	2
25 a	0900	16.7	2	14	2
25 b	1900	15.5	1	15	2 ^e

a - Day.

b - Night.

c - Activity pattern reversal--crabs moved into burrows, occurred in field at 12-14°C (see Figure 4).

d - Activity pattern reversal--crabs moved out of burrows, occurred in field at 12-15°C (see Figure 4).

e - Crabs dead in burrows.

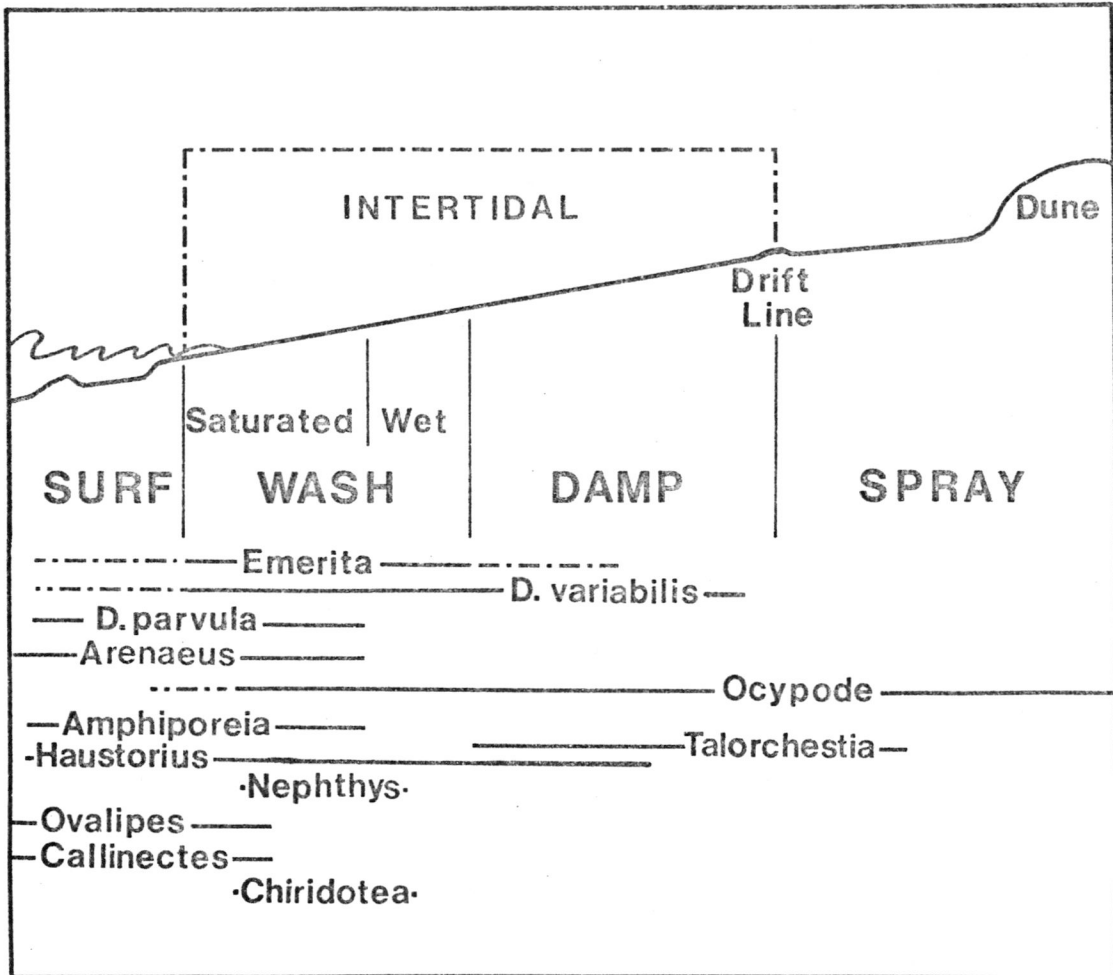


Figure 10. Vertical zonation of species on study beach. Broken lines represent areas utilized less frequently.

the mid wash zone while the haustoriid, A. virginiana, occupied the lower wash area. The haustoriid, H. canadensis, was generally found throughout the intertidal zone but at higher levels in the wash zone than A. virginiana. E. talpoida, D. variabilis, and D. parvula were typically located in the mid to low wash zone through August 1976. During subsequent months in 1976, and January of 1977, D. parvula were located offshore, while D. variabilis and E. talpoida were found at various levels in the intertidal zone and assumed to be offshore during coldest months.

O. ocellatus and C. sapidus were collected low in the wash zone and adjacent surf zone as was the sub-tidal crab, A. cribrarius, which may remain buried during daylight hours in waters close to shore. (In 20 years of trawling in deeper offshore areas, Dr. J. Costlow, of the Duke University Marine Laboratory, has rarely collected A. cribrarius (personal communication), while Dr. E. P. Ryan, of East Carolina University, has strung bait lines close to shore during the day which lured A. cribrarius out of their burrowed positions to feed on the bait (personal communication). Thus, it is likely that these portunids remain in the nearshore vicinity as adults.)

Variations in vertical distributions could be separated into those related to tidal or nocturnal migratory

patterns. The following seasonal migratory activity was observed in this study.

Tidal Migrations

Wash zone organisms maintain their position in the wash zone by migrating up the slope of the beach with advancing tides and down the slope with ebbing tides (Pearse et al., 1942; Hedgpeth, 1957). I observed these migrations occurring in the following species.

Emerita talpoida. -- Juveniles were found in low numbers, randomly dispersed, and swimming in the wash zone during winter months. By spring they had increased in abundance and size, were aggregated, and herds could be observed maintaining their position in the wash zone in the following manner. With each incoming wave, the herd would allow themselves to be washed up the slope of the beach. When wave momentum slowed, the herd would dig into the sand leaving only eyestalks and antennules exposed; then, as water gathered speed down the slope, they would feed with their long antennae as described by Efford (1966). When the backwash reached full momentum the entire herd would break at once from their positions and swim vigorously down the beach with the receding water.

Following recruitment to the beach in June first and second-year age classes were found vertically separated by

size in the wash zone and crowded together in a continuous band over the entire length of the study site and probably the entire length of the island. These bands exhibited a manner of wash zone activity similar to the spring herds, i.e., wash up the slope - dig in - feed - break and swim.

By late summer the activity pattern gradually began to change from breaking and swimming with each backwash to emerging from the sand, only after several waves had washed up the beach, and moving in the direction of tidal flow. On an ebbing tide in late September, I observed a unique activity not exhibited earlier by these organisms. After remaining buried long enough to become stranded in the wet zone, sections of the band up to 20 m in length would break from the sand in unison and run down the beach to the water where they dug in and remained until stranded again. This activity continued throughout the ebbing tide.

During fall months swimming activity was observed less frequently while stranding above the wet zone became common. It was difficult to find any Emerita on the beach during January 1977. By late February, young juveniles were found swimming in the wash zone while scattered herds of mature adults were back on the beach. No adults were seen swimming in the wash or nearshore surf zones during

winter months of 1976 or 1977. Most adults sampled in February and March were found stranded above the wash zone and buried in sand 10 cm deep. Others were found buried a similar depth in the wash zone. Not until mid spring were year old adults observed swimming in the wash or surf zone. Apparently adult Emerita do not migrate with the wash zone in winter.

Vertical distribution on the beach according to size, with youngest individuals at the top of the wash zone and oldest mature females further down the slope and into the surf zone, is characteristic of the genus (Weymouth and Richardson, 1912; and MacGinitie, 1938, for E. analoga; Alikunhi, 1944, for E. emerita). I observed this distribution pattern during summer and fall. However, during winter and spring months, prior to merging of herds into one continuous band in mid May, herds consisted of either juveniles or year old adults of approximately the same age group, as described by Efford (1965) for E. analoga, and intermixing of individuals from these uniform herds did not occur. Following intermixing of herds in late spring, the size gradient of larger individuals in lower wash zone to smallest at the top was apparently maintained by the ability of larger crabs to swim faster, and thereby farther in the backwash, than smaller crabs.

Donax. -- Both D. variabilis and D. parvula were observed migrating up and down the beach with the wash zone during winter, spring, and summer months. Populations were intermixed and both species allowed the surf wash to move them up or down the beach while extending the foot as a drag in order to stop and quickly dig in. Turner and Belding (1957) describe this activity in further detail.

In late summer, vertical migratory activity of both species ceased and D. parvula moved offshore while most of the D. variabilis population remained in the uppermost level of the intertidal zone, completely stranded except during high tide. The two populations remained separated in this fashion until mid March of the following year. At that time, only juveniles of both species were observed migrating with tidal fluctuations, while second-year adult D. variabilis remained in place high in the intertidal zone. No second-year D. parvula were found on the beach during this study.

Nocturnal Migrations

There were regular, predictable, seasonal migrations of the following macrobenthos into the wash zone at night.

Ocypode albicans. -- Overwintering adult ghost crabs left their burrows in the spray zone and entered the wash

zone to feed soon after dark from mid April to mid October 1976. They remained active in the wash zone and elsewhere on the beach throughout the night, retreating to their burrows or digging new ones at dawn. Overwintering juveniles were not observed in the wash zone during spring months although they were active in the spray zone at that time.

In mid October nightly migrations to the wash zone ceased and no further sightings of ghost crabs on the beach at night were made until the following spring. Burrow activity in the spray zone continued, though, for 8 weeks. During these 2 months, activity gradually tapered off from frequent sightings of crabs at the entrance of their burrows during warmer hours of the day, to complete absence of crabs from sight and filling in of the burrows with sand in mid December. No further burrow activity was evident until burrows reappeared in mid March of 1977. No crabs were observed outside of these spring burrows, however, until mid April when Ocypode were observed migrating into the wash zone at night.

Plaster casts indicated that the December burrows, which were constructed high on the beach near sand dunes, descended vertically to depths of at least 1 m, sometimes angling deep into the dune. Ocypode apparently overwintered deep in these burrows. Casts made from early

spring burrows averaged 90 cm in length and angled away from the ocean to a vertical depth in the sand of ca 70 cm.

Arenaeus cribrarius.-- These portunid crabs were observed feeding after dark in the wash and nearshore surf zones from late March to late November. They were generally observed slightly seaward of the wash zone, but during late summer and early fall were abundant high in the saturated zone, often buried into the sand leaving visible only eyestalks and a small portion of dorsal carapace.

Ovalipes ocellatus. -- These portunids were observed in the wash and nearshore surf zones from mid April to late July. They were typically found higher in the wash zone than Arenaeus during those times of year.

Biomass

Regression equations and r^2 values from regressions of ash-free dry weight (AFDW) on size are given in Table 3 for Emerita, Ocypode, Arenaeus, and Donax. Dimensions measured were shell length for Donax, carapace width for Ocypode, and carapace length for Emerita and Arenaeus. During the ashing process, gravid Ocypode data for all but two crabs were lost. Subsequently, the equation for non-gravid females was utilized for weight determinations of

Table 3. Regression equations and r^2 values from regressions of \log_{10} ash-free dry weight ($\log Y$) on \log_{10} size^a ($\log X$) for macrobenthos with five highest importance values.

Organism				
Genus	Type	Regression equation	Sample Size	r^2
<u>Ocypode</u>	Male	$\log Y = 3.12529 \cdot \log X - 4.27013$	n=11	0.942
"	Female	$\log Y = 3.14038 \cdot \log X - 4.35268$	n=12	0.936
"	Oviger	$\log Y = 5.50000 \cdot \log X - 7.93000$	n= 2	1.000
"	Juvenile	$\log Y = 3.54929 \cdot \log X - 4.92032$	n= 7	0.895
<u>Emerita</u>	Male	$\log Y = 2.37677 \cdot \log X - 3.77128$	n=15	0.936
"	Female	$\log Y = 2.56374 \cdot \log X - 3.79306$	n=26	0.977
"	Oviger	$\log Y = 2.73950 \cdot \log X - 3.92298$	n= 8	0.921
<u>Arenaeus</u>	Male	$\log Y = 3.90983 \cdot \log X - 5.41962$	n=11	0.985
"	Female	$\log Y = 3.16497 \cdot \log X - 4.09606$	n=13	0.928
"	Oviger	$\log Y = 3.24265 \cdot \log X - 4.18934$	n= 5	0.651
<u>Donax</u>	both species ^b	$\log Y = 2.61888 \cdot \log X - 4.86722$	n=30	0.983

a Carapace width for Ocypode, shell length for Donax, and carapace length for Emerita and Arenaeus.

b Determined for mixed samples of D. variabilis and D. parvula.

gravid Ocypode females. Relative differences in size-weight relations of these organisms are illustrated in Figure 11, in which regression equations for beach clams and female decapod crustacea are graphed. Though size ranges are similar for Donax and Emerita, Emerita clearly contributes far more AFDW for its size (i.e., has a smaller size:weight ratio) than Donax.

Seasonal fluctuations in AFDW are plotted in Figure 12, as determined for each sample date by the computer. Weights of individual organisms in these samples were predicted with the equations in Table 3. Maximum biomass values for D. parvula and Ocypode, collected in the intertidal zone, occurred 1 month prior to peak values for D. variabilis, Emerita, and Arenaeus populations. AFDW m^{-1} values for Emerita and Donax populations were typically 2 to 3 orders of magnitude greater than those for Ocypode and Arenaeus.

Growth and Recruitment

Size-frequency histograms are given in Figures 13 to 16 for species with the top five ranked importance values.

Emerita talpoida

Initial recruitment of Emerita occurred during January, with a second recruitment in June and a third wave beginning in August and building through December (Figure

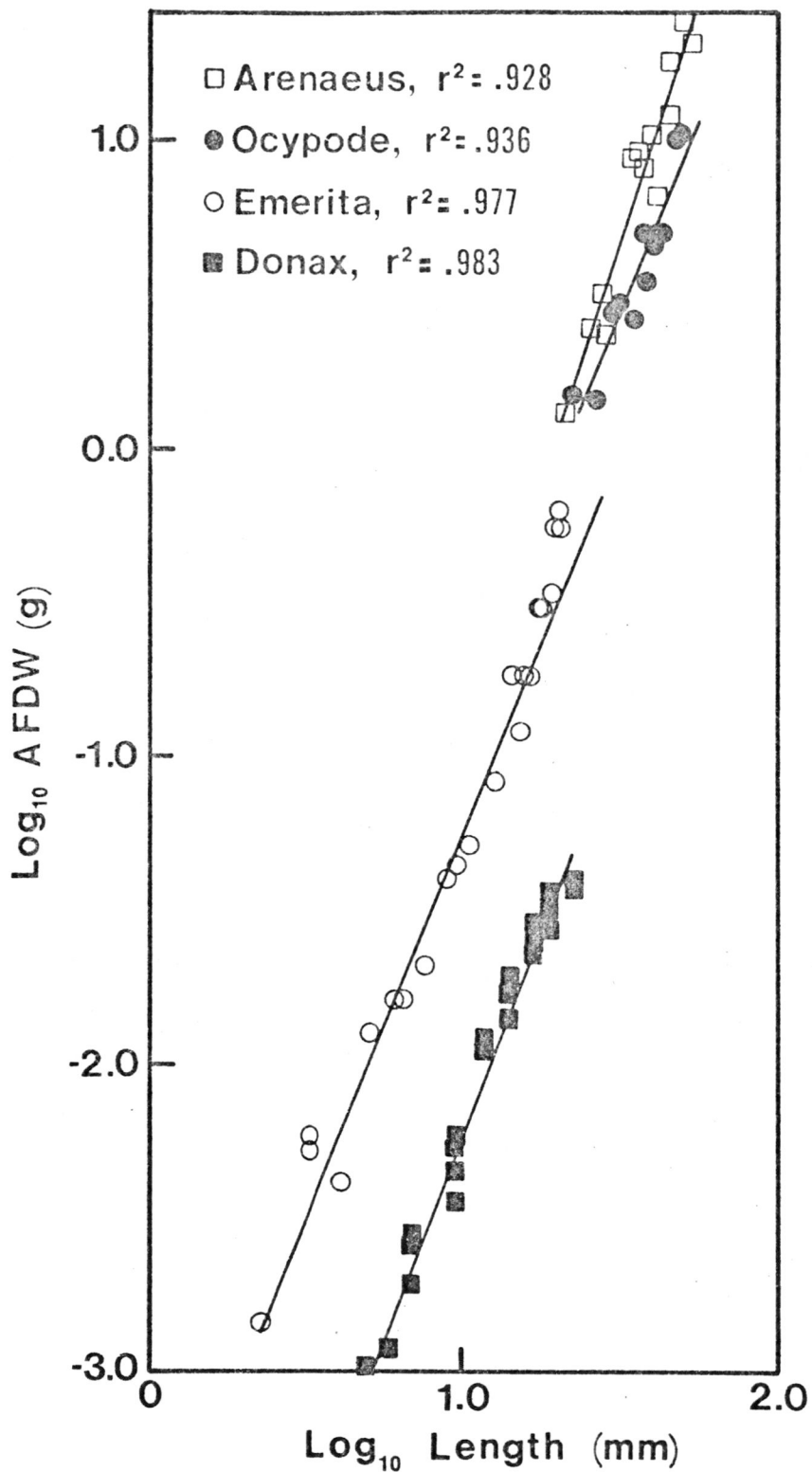
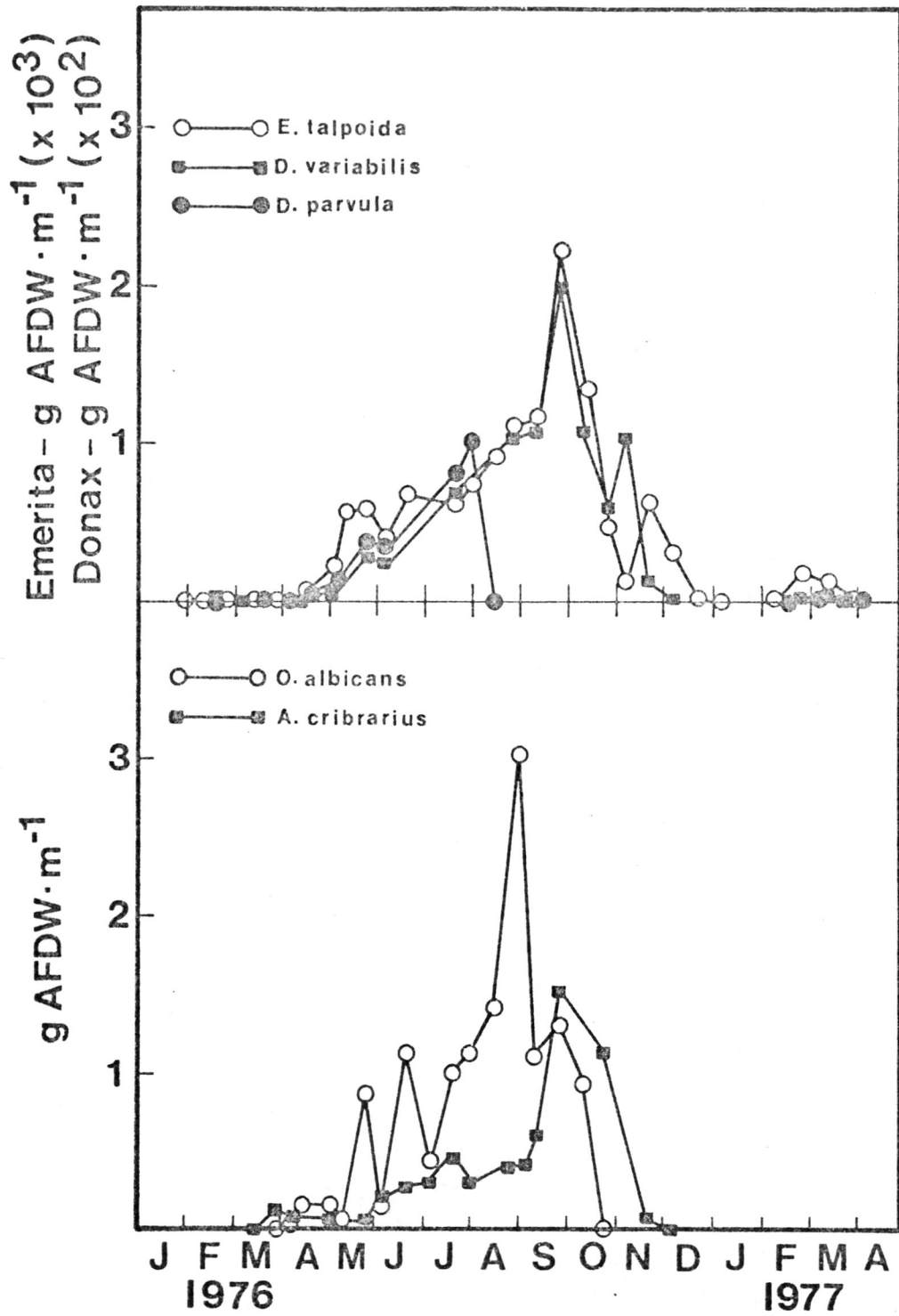


Figure 11. Comparisons of size:weight relationships (g AFDW vs mm shell size graphed as log_{10}) based on (female) decapod and clam regression equations given in Table 3.

Figure 12. Comparisons of AFDW of species with top five importance values as related to time of year.



13). Ovigiers were present in March and continued through August.

The protandric hermaphroditism suggested by Barnes and Wenner (1968) for the West Coast species, E. analoga is not apparent for E. talpoida. Rather than sex reversal and subsequent further growth as females, it appears that males begin to "bunch up" in the upper male size classes during September, October, and November (Figure 13). Thus, it appears here that growth in males tapers off and stops at a maximum carapace length equal to about half that of females.

Donax

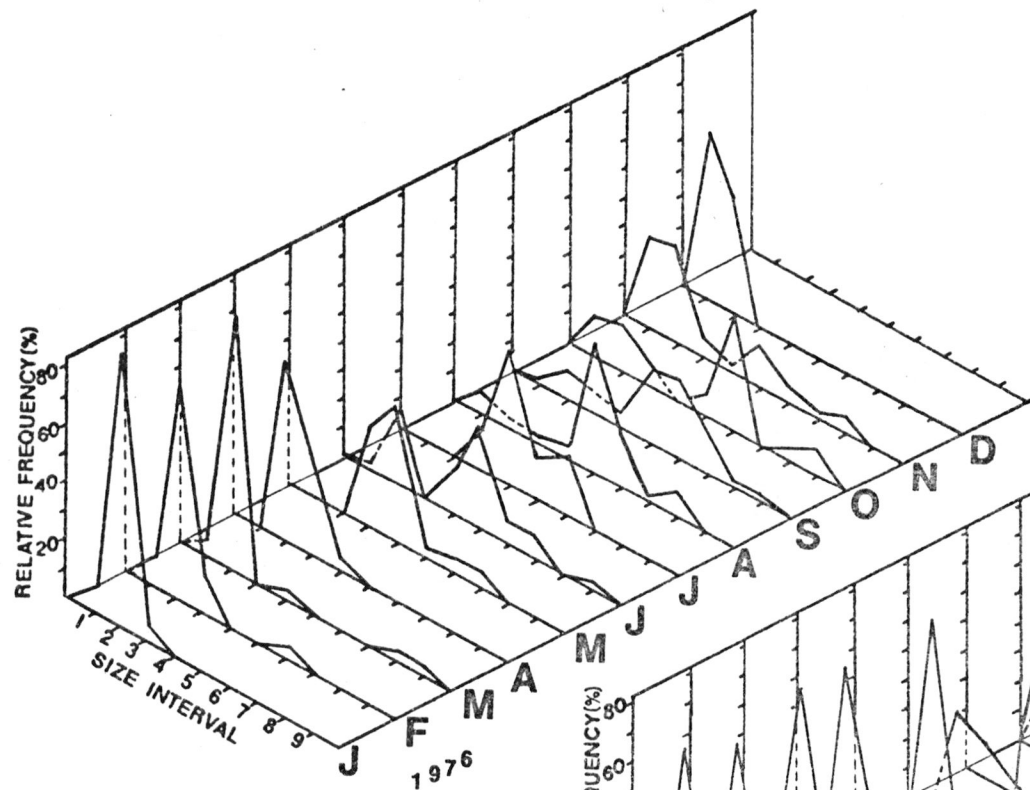
Recruitment of D. variabilis occurred in February and November while only a February recruitment of D. parvula was observed (Figure 14). Adult D. variabilis returned to the beach in February after overwintering offshore. There was an obvious difference in size between these two populations during July and August. While at least a 2 year life span is indicated here for D. variabilis, no second-year D. parvula were apparent.

Ocypode albicans

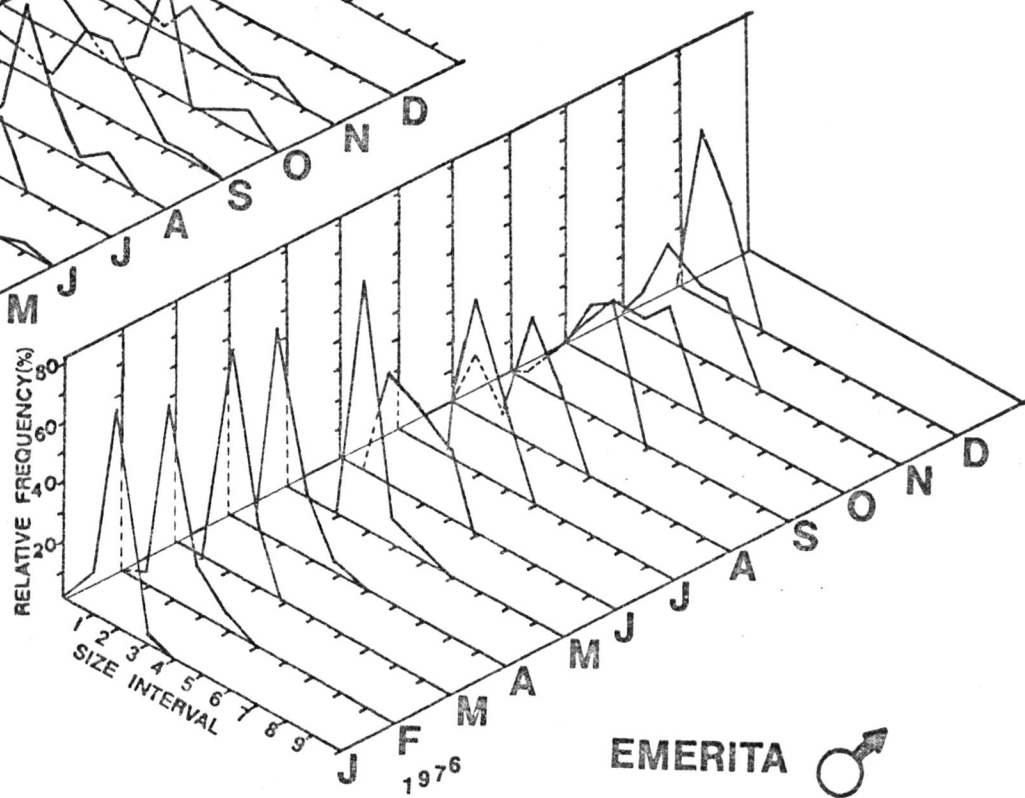
Initial recruitment occurred in low numbers in late spring (Figure 15). This phase does not appear on the graph in Figure 15 since these early juveniles did not

Figure 13. Size frequency distribution polygons for male and female Emerita talpoida collected during 1976.

Legend:	1(0-3.5)	4(9.6-12.5)	7(18.6-21.5)
Carapace	2(3.6-6.5)	5(12.6-15.5)	8(21.6-24.5)
Length (mm)	3(6.6-9.5)	6(15.6-18.5)	9(24.6-27.5)



EMERITA ♀



EMERITA ♂

Figure 14. Size frequency distribution polygons for Donax variabilis and Donax parvula collected during 1976 and 1977.

Legend:	1(0-6.0)	4(11.1-13.5)	7(18.6-21.0)
Shell	2(6.1-8.5)	5(13.6-16.0)	8(21.1-23.5)
Length (mm)	3(8.6-11.0)	6(16.1-18.5)	9(23.6-26.0)

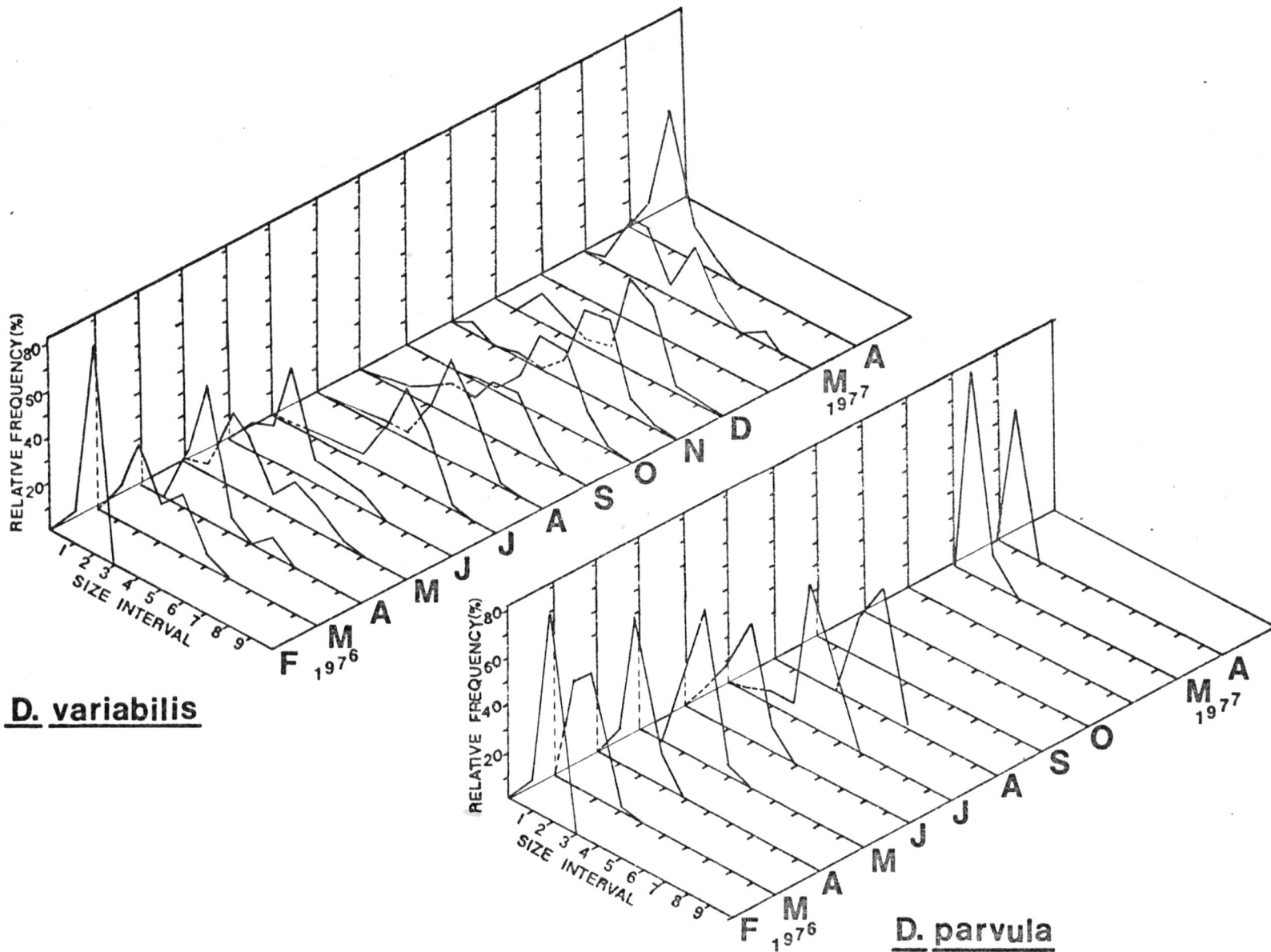
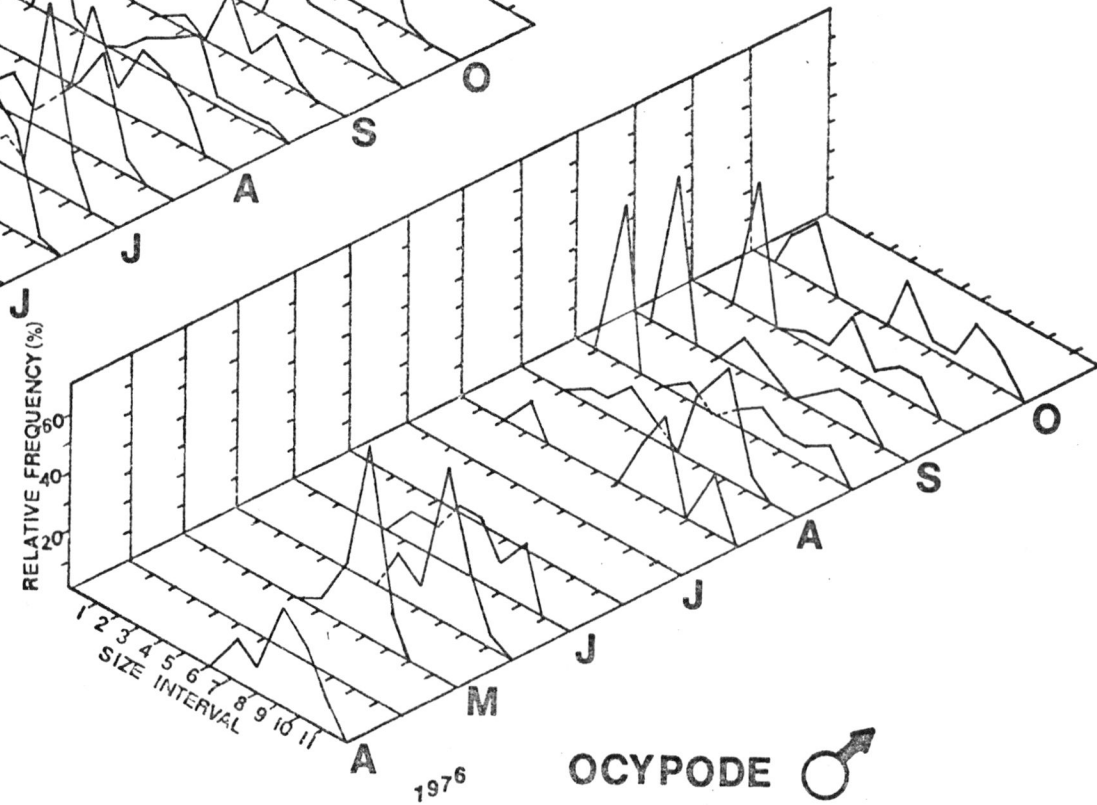
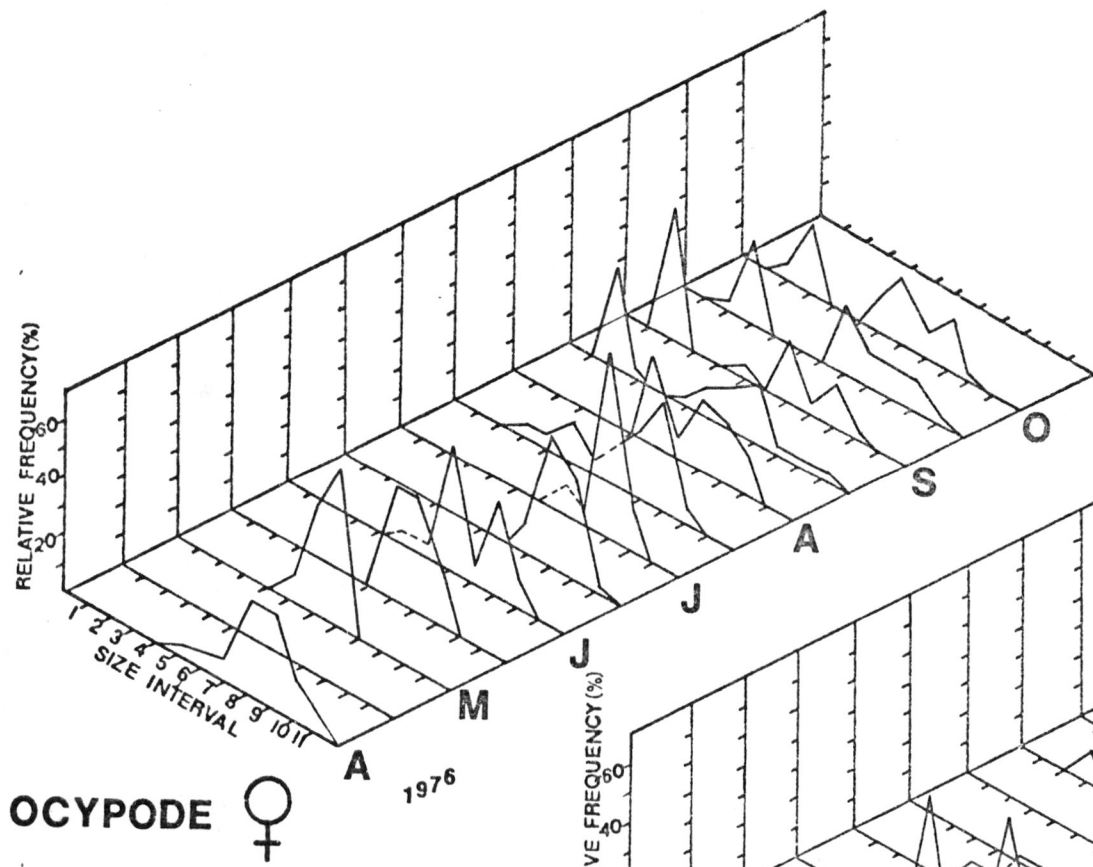


Figure 15. Size frequency distribution polygons for male and female Ocypode albicans collected during 1976.

Legend:	1(0-4.9)	5(20.0-24.9)	9(40.0-44.9)
Carapace	2(5.0-9.9)	6(25.0-29.9)	10(45.0-49.9)
Width (mm)	3(10.0-14.9)	7(30.0-34.9)	11(50.0-54.9)
	4(15.0-19.9)	8(35.0-39.9)	



migrate to the wash zone where crabs were collected for measurement. Crabs representing smaller size classes began migrating from spray zone to wash zone in mid July. A large recruitment occurred during a short period in mid August. No subsequent recruitment occurred until the following spring when juveniles were spotted on the high beach in low numbers (Frank Reilly, personal communication). Ovigiers were present from June to late September. Though males were present on the beach during late June and early July, sample sizes were too small (less than five) to be effectively graphed.

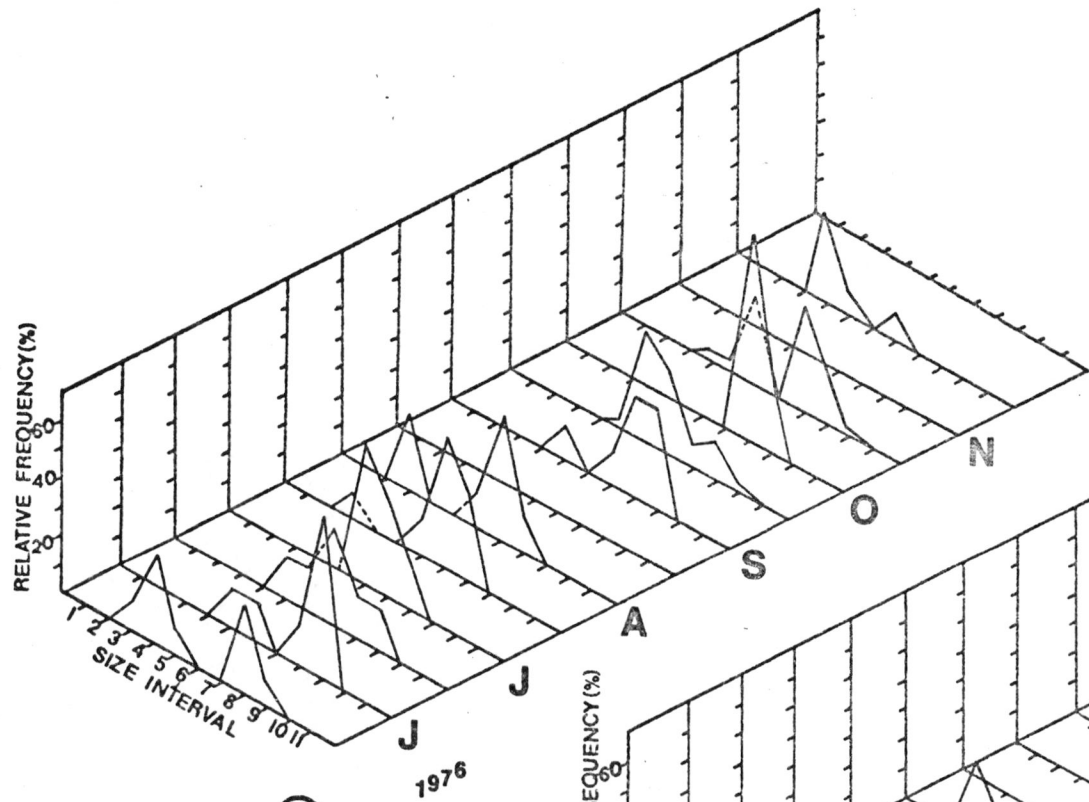
Arenaeus cribrarius

No juveniles smaller than 15 mm carapace length were observed on the beach or nearshore waters in this study (Figure 16). Thus, it appears that early post-megalops forms do not migrate to the wash zone. However, larger juveniles were present in all samples, except in early October. Highest frequencies of juveniles occurred in late May, early August, and mid November.

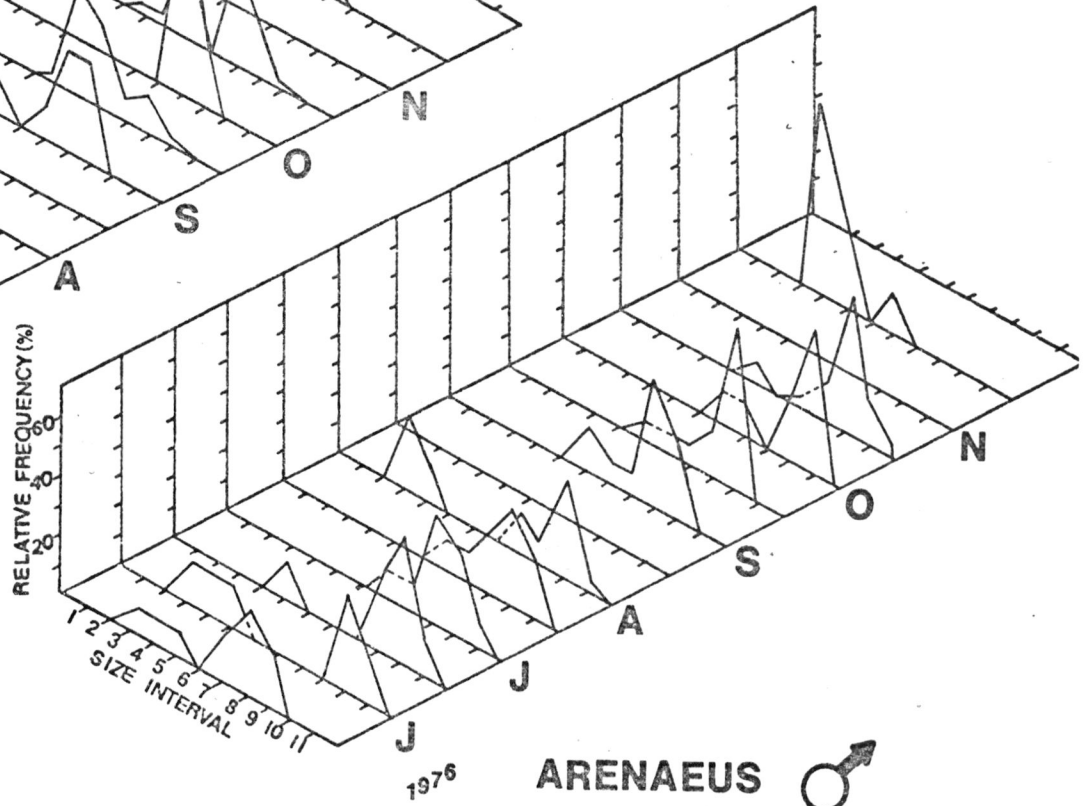
The pubertal molt occurred in females at a carapace length of ca 40 mm. Largest juveniles encountered were 40.0 to 42.0 mm carapace length while the 67 adult females measured in this study ranged from 40.6 to 59.1 mm in length, with a mean of 48.5 ± 3.59 mm. Based on a percent

Figure 16. Size frequency distribution polygons for male and female Arenaeus cribrarius collected during 1976.

Legend:	1(0-15.0)	5(30.1-35.0)	9(50.1-55.0)
Carapace	2(15.1-20.0)	6(35.1-40.0)	10(55.1-60.0)
Length (mm)	3(20.1-25.0)	7(40.1-45.0)	11(60.1-65.0)
	4(25.1-30.0)	8(45.1-50.0)	12(65.1-70.0)



ARENAEUS ♀



ARENAEUS ♂

size increase of about 33 with each molt, which is displayed by the closely related C. *sapidus* (Churchill, 1919), size of a typical female following the pubertal molt would not be expected to reach 59 mm in length. These data, and observations of several doublers with males cradle carrying adult females, indicate there may be at least one post-pubertal molt in *Arenaeus*.

Doubler is the term describing a male crab cradle carrying a female beneath him by hooking his first walking legs and chelae between the first walking legs and chelae of the female. The crabs remain attached for 2 or more days until the female molts at which time mating occurs (Van Engle, 1958, for *C. *sapidus**). I observed *Arenaeus* doublers in June through October samples, with highest frequency of doublers (75% of crabs taken) occurring in October. Ovigerous females were present in samples from mid June through mid July.

Predation

Crabs

*Arenaeus *cribrarius**. -- At night this crab moved up onto the beach to feed on *Emerita* and *Donax*. It found its prey by digging into the sand with its first two pairs of walking legs. I observed it feeding on *Donax* more frequently than on *Emerita*.

Ocypode albicans. -- These crabs spent most of the night in the wash zone feeding on both Emerita and Donax. I was able to observe this activity from close range (within 1 m). To locate prey in the wash zone, Ocypode dug in the sand, alternating strokes of the two chelae down and away from the body while opening and closing its pincers. When feeding on Donax, the crab first cracked the clam shell open with its large chela. All but the dorsal carapace of Emerita was eaten. Verrill and Smith (1874) observed ghost crabs feeding on Talorchestia megalopthalma.

Ovalipes ocellatus. -- This portunid was observed eating Donax in the wash zone at night.

Fish

Seining attempts continually produced low yield due to waves emptying the seine, but during peak densities in late summer, fish could easily be collected with a dip net. The following observations were made from fish collected by both methods.

Menidia menidia. -- Schools of silversides were often observed during both day and night sampling in the wash zone. Stomachs commonly contained small Donax.

Menticirrhus americanus. -- Stomachs of whiting were generally packed with Emerita. These fish were abundant in the surf and low wash zones at night, especially during summer and fall. During nearshore surf zone collections in summer and fall, densities of whiting were so high that they commonly slapped against my legs as I walked through the surf.

Paralichthys denatus. -- Summer flounder were observed in surf zone trenches close to shore in late summer and fall. Stomach contents of the three flounders examined all contained Emerita.

Trachinotus carolinus. -- Pompano were observed in the wash zone during summer and fall months. These fish would swim high up the slope of the beach, laying almost flat on their sides in the wave wash. Stomach contents revealed they were feeding on Donax.

Birds

Several species of beach birds were present during the study. I observed unidentified species of plovers and sandpipers feeding on Emerita. Loesch (1957) observed the sanderling, Crocethia alba feeding on Donax. Gulls and oyster catchers are known to prey on beach clams (Pearse et al., 1942).

Mammals

I found on several occasions raccoon tracks along the tops of dunes and leading down into the intertidal zone. Raccoon would seem a likely predator of Donax, Emerita, and Ocypode.

Commensalism

An epizoic hydroid, Clytia bakeri, grows on the posterior end of the shell of many species of Donax (Loesch, 1957). I observed Clytia sp. growing on up to 3% of Donax sampled during the period 6 June to 14 August 1976.

A profuse growth of Clytia sp. was found attached to an old female Arenaeus, 51. mm in length, on 3 September 1976. The hydroid was attached to the crab's only chela and along the anterolateral portion of the dorsal carapace. A number of small barnacles were also located on the carapace of this crab.

DISCUSSION

The sandy beach in this study does not comprise a single discrete community with definable barriers. It is, rather, a composite of three adjacent and functionally interdependent communities--the upper beach, wash zone, and nearshore region. These can be united into one category and classified by numerically dominant and metabolically important species. Environmental stresses acting on this high energy beach have "directed" adaptations which enhance species interactions, coexistence, and thus stability within this composite system. Limiting factors operating in this ecosystem are substrate stability, temperature, and possibly space.

Interactions among these communities have not been closely examined. They appear here to be coupled through interrelationships in trophic structure and habitat utilization.

Trophic Structure

Lacking a resident autotrophic community capable of supporting a complex trophic structure, the high energy sandy beach is functionally heterotrophic. The floral communities present on ocean beaches, primarily diatoms attached to sand grains, are kept at relatively low levels by wave action, as indicated by Steele and Baird (1968)

who found that yearly primary productivity for an ocean beach in Scotland was only 4 to 9 g C m⁻². Thus, beach fauna must depend almost entirely on inputs from adjacent communities as an energy source.

Allochthonous imports of organic detritus and plankton are the base of intertidal food webs. Fox (1950) examined inshore (damp zone) detrital metabolism on the Scripps Institute beach in California and concluded that on sandy beaches, detrital dynamics functionally control inshore metabolism and that population sizes in marine inshore areas are directly proportional to the quantity of detrital input. Whereas Fox was dealing with infauna located high in the intertidal zone, in the present situation planktonic imports play an important role as well as detritus in the wash zone.

Efford (1966) reviews feeding in Emerita and portrays it as a passive filter feeder which ingests a variety of protozoans, algae, some larger planktonic forms, and bacterial-detrital aggregates "... about what would be obtained by unselective straining of the water along the shore." The suspension feeding Donax populations found associated with Emerita most likely utilize the same raw food source while they are active in the wash zone.

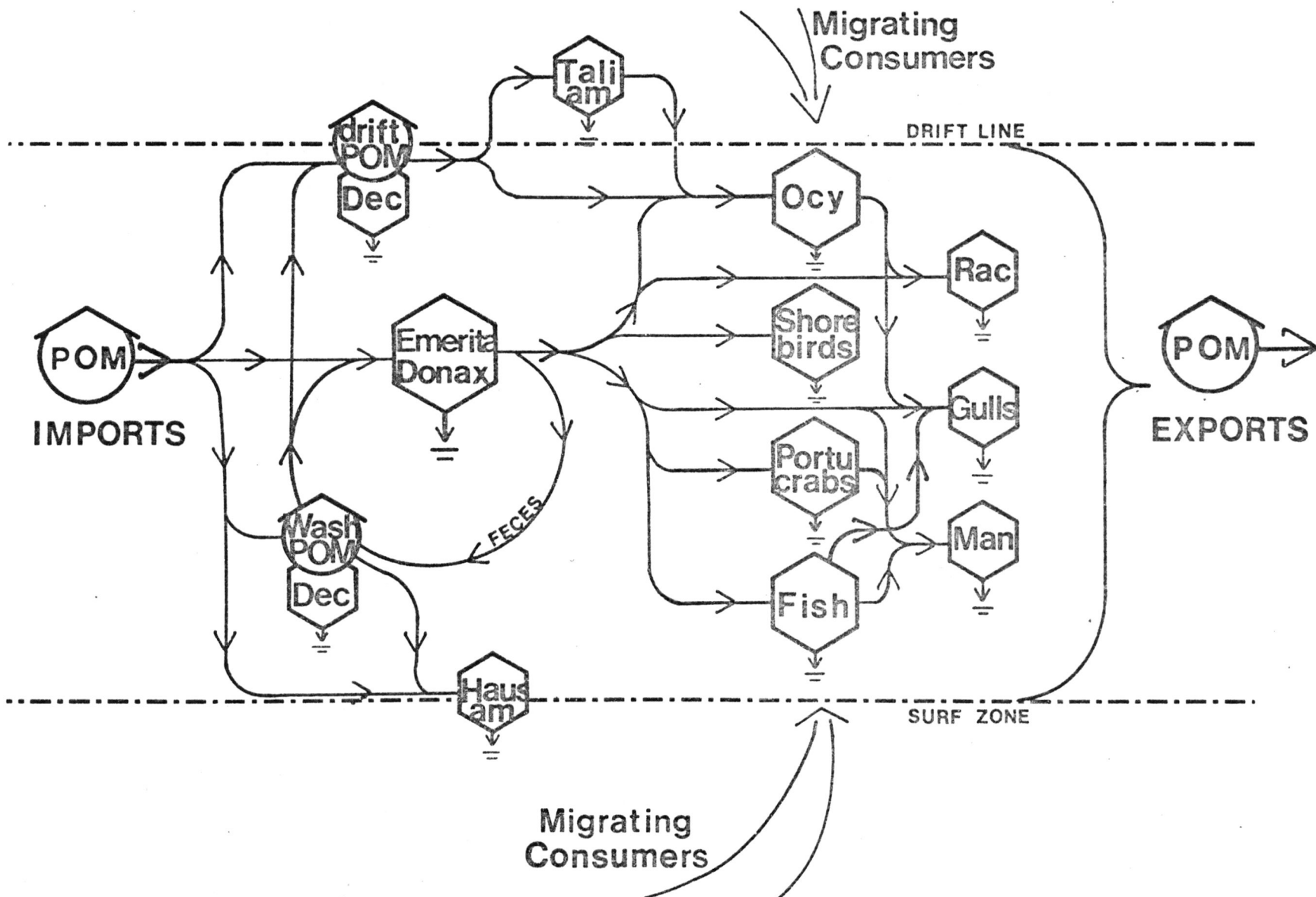
Considering sandy beach trophi-dynamics on Bogue

Banks, organic detrital and planktonic imports enter this open system as suspended particulate organic matter (POM), the detrital portion associated with bacterial decomposers (Figure 17). This POM-decomposer complex is partitioned into wash zone and drift line compartments, and subsequently utilized as a food source by grazers with appropriate feeding mechanisms. The most important of these grazers or "primary consumers" are Emerita and Donax through which flow a major portion of the energy utilized at this level. These organisms are the primary link between the otherwise unavailable POM and higher-order consumers in the sandy beach ecosystem.

Higher level positions in the food web are filled by trophic generalists (opportunistic scavengers and predators) which migrate to the intertidal wash zone from adjacent communities to tap this readily available resource. Incidentally, man is included here; Emerita are used as bait, Donax (Coquina clams) make a delicious soup (Drucy Aloveria, personal communication), and fishermen are attracted to this beach by fish in the surf zone. It is significant here that none of these higher-order consumers (except gulls and occasionally man) are present on the beach during those winter months when Donax and Emerita have migrated offshore.

It appears that if both Emerita and Donax populations

Figure 17. Qualitative trophic model illustrating energy flow through the sandy beach ecosystem. This open system depends on particulate organic matter (POM) imports which are stored in drift line and wash zone POM-decomposer (Dec) complexes. Energy flow to upper trophic levels is primarily through Emerita and Donax, but POM-Dec complexes are also utilized by talitrid amphipods (Tali am) and haustoriid amphipods (Haus am). Upper level consumers consist of ghost crabs (Ocy), shore birds, portunid (Portu) crabs, and fish which migrate to the wash zone to feed; and above these, raccoon (Rac), gulls and man.



were scarce, the beach could neither support the large populations of Ocypode nor attract the high density of fish observed feeding in the wash zone during this study. At least two mechanisms appear to be involved in maintenance of this major energy pathway. There is (1) an alternate source of prey if environmental stresses adversely affect one or the other of these two primary consumers, and (2) operation in late summer at carrying capacity levels with larval recruitment to buffer predatory losses.

Energy losses in the ecosystem occur at each level of the trophic structure. Initial losses due to unutilized POM are exported by longshore and nearshore currents horizontally down the beach and into subtidal and deeper waters offshore (Hedgpeth, 1957). Fecal losses would contribute also to exported POM. Additional energy losses would include unharvested primary consumers, prey consumed by transient species, and respiratory heat losses at all levels. Meiofaunal populations are classed here as unavailable energy and are considered insignificant to the benthic community. Several researchers believe they compose a completely separate system with little or no interaction between the two (McIntyre, 1969; Cox, 1976).

Standing crop estimates of major primary consumers and higher order benthic consumers for late September 1977,

are presented in Table 4. A complete survey of both shore birds and fish is needed to complete this illustration of relative compartmentalized energy storage. One beach bird per meter of beach length is a conservatively high estimate made for that date, while fish populations were at least an order of magnitude higher. At any rate, standing crop estimated for primary consumers in July, August, and September was obviously large enough to support a considerable amount of predation.

The greatest pathway of energy flow on the sandy beach appears to be directed through grazers and up into higher level consumers which migrate in from adjacent communities. This system integrates offshore and upper beach communities with the wash zone and enables an efficient trophic exchange of otherwise unavailable energy through the specialized converters, Emerita and Donax. In contrast, on a low energy shore such as that in a marsh area, energy flow through detrital pathways should predominate. The accumulation of detritus and fine silt particles in such a system is similar to the litter layer on a forest floor through which 90 percent or more of the net primary productivity is utilized through detrital dynamics (Odum, 1971).

Although predation on beaches has been described for particular prey (Pearse et al., 1942 for Emerita; Loesch,

Table 4. Standing crop estimates of major macrobenthic grazers and predators for July, August, and September 1976.

Species	AFDW·m ⁻¹ beach frontage ^a		
	31 July	28 Aug	25 Sept
Grazers			
<u>Emerita talpoida</u>	754.4	1013.0 ^b	2201.2
<u>Donax variabilis</u>	97.4	105.0 ^b	200.2
<u>Donax parvula</u>	104.5	- ^c	- ^c
Totals:	956.3	1118.0	2401.4
Predators			
<u>Ocypode albicans</u>	1.1	3.0	1.3
<u>Arenaeus cribrarius</u>	0.3	0.4 ^b	1.5
Totals:	1.4	3.4	2.8

^a Determined per meter beach frontage of intertidal zone.

^b Estimates from Figure 12.

^c Located offshore.

1957 and Wade, 1967 for Donax) the importance of Emerita and Donax to beach communities has never been fully realized. Pearse et al. (1942) noted that "...rapid turnover and growth of Emerita make it an important source of flesh." But in the recent Coastal and Offshore Environmental Inventory, Pratt (1973) reduces the "value" of beach fauna to "...small, consisting mainly of providing a source of food for shore birds." In contrast, the present study has demonstrated (Figure 19) the importance of Emerita and Donax in providing a major link between primary producers and other particulate organic matter and higher trophic levels. Also, these grazers link energy exchange pathways between zones on the beach.

Habitat Utilization

Few species are adapted to the stress conditions of desiccation, temperature variation, shifting substrate, and pounding surf encountered on sandy shores. Foremost in importance among adaptations are rapid burrowing capability, ability to respond to tidal fluctuations, and a specialized respiratory system. But the key factor involved in the coexistence of several species in this harsh environment is the stratification of the ecosystem into several sub-habitats or zones. As Abele (1974) has pointed out, "a species can use one substrate (zone) as a shelter, another as a feeding site, and another as a

source of nutrition, thus reducing competitive interactions for each one." Furthermore, use of each zone on the sandy beach is temporally separated into day and night use as well as high and low tide use, while spatially separated as a result of the vertically migrating wash zone. This complexity of sub-habitats favors increased niche diversity which is necessary in order to support several species on a homogeneous substrate.

One value of stratification to the beach ecosystem is illustrated by the Emerita-Donax interaction as follows. The most productive region on the sandy beach appears to be the wash zone. At least three species, Emerita, D. parvula, and D. variabilis, demonstrate a preference for and are able to coexist in this relatively confined area during late winter and spring months (Figure 6). All three play an important role in the trophic structure of the ecosystem. Regarding spatial requirements, Emerita appears to be a specialist preferring a relatively small realized niche, the wash zone, and capable of operating at or near its population carrying capacity. Both species of Donax are spatial generalists and occupy a broad realized niche, including both wash zone and adjacent communities. As densities of all three populations peaked in August 1977, there was either a period of intense spatial competition or perhaps some form of antibiosis by Emerita.

At this time, apparently out competed for space, D. parvula moved to the nearshore community while D. variabilis became stratified high in the damp zone during ebbing tides. Emerita remained active in the wash zone. This stratification enabled all three species to remain associated with the ecosystem. D. variabilis and Emerita remained in the intertidal zone for the remainder of the year, temporally separated except for brief periods during high tide. D. parvula survived this hypothetical stress situation by moving into the adjacent nearshore community. Through this overlap in habitat use, stability in the ecosystem was maintained.

If the hypothesis that space is a limiting factor late in the season is correct, then competition among these wash zone species is moderated by intra-community habitat utilization thus allowing coexistence of these organisms in the ecosystem to continue.

Further interrelationships among these communities is evident though not necessarily caused by competition (Figure 10). The nearshore community is an important winter refuge for Emerita and Donax when temperatures drop in the wash zone (Edwards and Irving, 1943, for Emerita; Morrison, 1971, for Donax). And several organisms migrate across community boundaries regularly to feed (Figure 17).

If we regard niche specifications (habitat utiliza-

tion as well as trophic role) of beach organisms in a functional sense, then nearshore, wash zone, and upper beach biota cannot be considered to comprise discrete communities in those areas. The sandy beach ecosystem is biologically organized. It appears here as a functional composite of three adjacent communities which blend to yield maximum utilization of available resources. Any one of the three communities could not be understood without considering the other two.

Yet much of the literature concerning sandy beaches is centered around only one or two of these communities. Dahl (1953) emphasized only the intertidal zone, neglecting portunid crabs and fish completely in his notable work concerning worldwide ecology and zonation of beach fauna. More recently Gauld and Buchanan (1956), Rodriguez (1959), and Dexter (1969, 1972) have followed the same pattern of describing community structure on sandy beaches in terms of intertidal fauna only and excluding such organisms as birds, fish, and portunid crabs from positions in the community.

There is a paucity of data concerning nearshore portunid and fish populations on sandy shores. These predators are involved in strong relationships with wash zone populations (Figure 17) and may have a marked effect on their densities. Future studies of beach communities

are encouraged to consider the beach in its entirety, as an integrated composite of nearshore waters, wash zone, and upper beach.

Ecosystem Stability

In any attempt to understand an ecosystem in functional terms, a seasonal approach is mandatory. Further, to determine whether the system is inherently stable and reproducible, and thereby validate any functional classification, other factors must be considered.

McNaughton and Wolf (1973) define ecosystem stability as (1) persistence of certain relative abundance relations through time, (2) persistence of certain species combinations through time, and (3) ability of the community to maintain its functional organization following an external perturbation. Odum (1971) augments this definition with the "pulse stability" concept explaining that intertidal regions, for example, are maintained in early, fertile stages of community development by (a) tides which provide energy for rapid nutrient cycling, (b) complete community adaptation to the intensity and frequency of perturbations (i.e. temperature changes, tidal exposure), and (c) population life histories coupled to periodicity.

The fact that reproducibility of relative abundance relations varies from year to year on beaches is borne out

by Coe (1955) who found Donax on a California beach abundant during some years and rare others, and by this study where Emerita densities were about an order of magnitude greater than those in Diaz's (1974) study on the same barrier island. Thus the magnitude of numerical dominance by Emerita could vary considerably from year to year.

Regardless of density fluctuations stability is evident here. The biotic organization on this beach appears to remain intact from year to year. The species assemblage collected during this study is basically the same as that collected on outer beaches of Bogue Banks 35 years ago by Pearse et al. (1942). More recent literature also reports certain of these organisms on Bogue Banks. The haustoriid amphipods present in this study were observed by Dexter (1967) on Bogue Banks about 10 years ago. Donax populations have been described in this area by Dexter (1969) and Porter (personal communication). Diaz (1974) studied Emerita population dynamics on Bogue Banks three years previous to this effort, and though densities appear lower in the former study, abundance peaks as well as recruitment to the beach graphed for the present study (Figures 7 and 13) are almost identical to Diaz's graphs. Arenaeus populations have been observed in the wash zone along Bogue Banks during recent years

(Costlow, 1975, personal communication) and I found them especially prevalent along with Ocypode in September of 1975, prior to this study. Furthermore, each species described in this study (with the exception of Amphiporia, Callinectes, and Chirodotea) are listed as "common animals" on Bogue Banks by the Duke University Marine Laboratory Reference Library (Kirby-Smith and Gray, 1973).

Certain species interactions further contribute to stability of the beach ecosystem. The reliance of higher order consumers on primary consumers in this community has already been emphasized. Furthermore, Donax supports at least one epizoite, Clytia, through a commensalistic relationship. This could be regarded as an isolated process of community succession in which Donax populations offer a more stable substrate for colonization.

There appears to be a high degree of pulse stability on this beach. Adaptations to the intensity and frequency of perturbations are evident throughout the community. Migratory activity in Emerita, Donax, and haustoriid amphipods is intimately coupled with tidal fluctuations during most of the year. In response to extreme temperatures, organisms are able to burrow into warmer substrate depths where temperature changes are moderated (Figure 5); this is particularly evident in Ocypode and Emerita which were shown in this study to burrow deeper in winter months.

Desiccation tolerances are high; Ocypode can survive in damp sand (Wolcott, personal communication), while Emerita and Donax are capable of withstanding long periods of stranding in the damp zone as indicated in this study. Niche specifications are broad, allowing emigration to more stable habitats during times of severe environmental stress. This is supported here by the complete migration into the nearshore community by Emerita and Donax, and dormancy of Ocypode deep in the sand, during colder months, followed by their return to the beach when temperatures rose.

Life histories are coupled to periodicity through reproductive, recruitment, and population growth phases. Reproductive periods appear timed so that recruitment will occur on the beach under optimal environmental conditions for each species. Emerita ovigers were present as early as March with larval recruitment to the beach in June (Figure 13). A subsequent recruitment began in August and increased in magnitude through December. Similar patterns of recruitment (without the June stage) are evident in Donax (Figure 14) and Ocypode (Figure 15) populations. Each population is thus provided a diverse age distribution during overwintering which probably increases chances of survival through the winter months. Furthermore, larval recruitment stages are obviously of

sufficient duration to allow for uncertainties of near-shore and longshore current fluctuations (Hedgpeth, 1957).

Population growth is cyclic. There is a pattern of seasonal succession of appearance on the beach (Figure 6), apparently in phase with cyclic temperature changes (this annual seasonal succession should not be confused with the term community succession). This pattern appeared to begin to repeat itself during the final months of this study (winter and early spring of 1977).

Thus it is apparent that a relatively high degree of ecosystem stability exists. High standing crop yield is evident for grazers (Table 4). Organisms display a great deal of adaptation to environmental conditions and biota appear to follow an annual pattern of seasonal succession. There appears to be sufficient support here to state that reproducibility of biotic assemblages is high from year to year. Thus characterization of this ecosystem in terms of the important species in this study is warranted.

The dominant species, Emerita and Donax, should be given top priority in any attempt to classify this particular beach. They are metabolically important to this system through their unique role as major energy converters. They endow an enormous amount of biomass to a system operating under a high degree of natural stress and thus contribute significantly towards ecosystem stability.

Through adaptations such as burrowing and migratory capabilities (both tidal and intra-community) they have become well suited for life on sandy beaches and are, in fact, unique to sandy beach ecosystems (Williams, 1965, for Emerita; and Morrison, 1971, for Donax). Furthermore, they should receive primary attention in environmental assessments and other studies regarding the effects of man's activities on sandy beaches, such as beach nourishment and deposition of dredge spoil.

Species Diversity

The importance of studying beach communities during various seasons cannot be overemphasized. It is obvious from Figure 9 that one could describe an essentially different biotic assemblage during each of the four seasons. Furthermore, a complete understanding of interspecific and intra-community interactions is not obtainable in a short term study. Diversity parameters are often determined without regard for seasonality. These can lead to poor comparisons and misrepresentation if not qualified. The effects of seasonal successional trends on sandy beach diversity is examined here through a number of parameters. A review of the applications and calculations of these parameters is given by Livingston (1976).

The combined effects of numerical dominance by Emerita

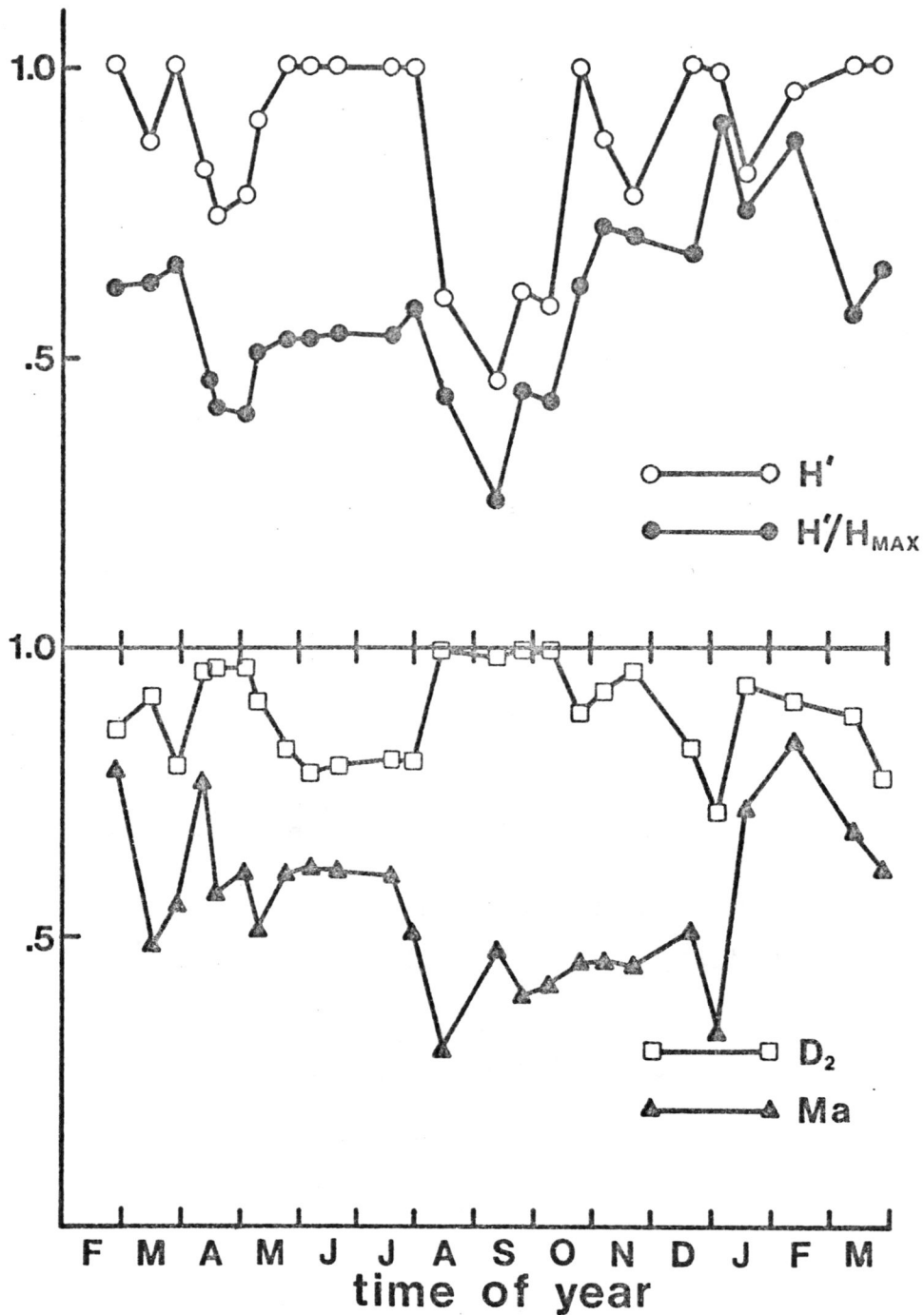


Figure 18. Seasonal changes in Shannon-Weaver (H'), Pielou equitability (H'/H'_{MAX}), and Margalef (Ma) indices for macroinvertebrates taken on Bogue Banks. Relative dominance (D_2), included here, is based on combined relative abundance of the two most abundant species.

and the emigration of D. parvula and Ovalipes induce a dramatic decline in diversity in late summer (Figure 18). This August decline is apparent in graphs of Margalef's (1958) species richness, Ma , and Pielou's (1969) equitability (evenness), H'/H'_{max} , with a subsequent climb in relative dominance, D_2 , of the two most abundant species, Emerita and D. variabilis on the beach at this time. Both Ma and H'/H'_{max} are components of the Shannon-Weaver informational index (Shannon and Weaver, 1963), H' , which subsequently decreases. Though Ma increases in mid September due to the appearance of Callinectes and re-appearance of Haustorius (Figure 6), H' continues to decline with H'/H'_{max} as complete numerical dominance by Emerita occurs in phase with the population surge in mid September of this species (Figure 7).

Other diversity fluctuations are due primarily to population oscillations early in the year and dominance shifts in January from warm (Emerita, Donax) to cold tolerant species (Haustoridae). The only period of relative diversity stability appears during June and July, apparently a time of minimal interspecific and environmental stresses. Shannon-Weaver indices during this time (1.05) are similar to that (1.02) given for a Pacific (quartz) sandy beach in Panama during the same time of year by Dexter (1972). Dexter's H' values were twice

as high (2.23) on an Atlantic Panamanian beach composed of calcareous sand. It is likely that this variation on the calcareous beach could be attributed to differences in substrate characteristics. These H' values for quartz sand beaches are low compared to those values typical for other marine habitats.

In contrast with terrestrial communities, maximum diversity would not be expected to increase on a tropical sandy beach over that for a temperate sandy beach since niche availability is limited in both systems by wave energy and a constantly shifting substrate. Rather than increasing diversity along a gradient from temperate to tropical sandy beaches, there is replacement of species in favor of those better adapted to warmer environments (Dahl, 1952). Thus valid comparisons between diversity on Bogue Banks can be made with that on beaches in Panama. The high H' value for the calcareous Panamanian beach compared with those given for the Panamanian and Bogue Banks quartz beaches emphasizes the importance of substrate characteristics to the ecosystem.

Another method for estimating diversity is to plot cumulative percent composition against species rank as described by Sanders (1968). This measure of numerical quality among species, or "dominance diversity," in the community is determined here for both abundance and

importance values (Figure 19). The 79.2 percent deviation of the abundance curve from theoretical maximum diversity is due to the overall dominance in numbers by three species, Emerita, D. variabilis, and D. parvula. Considering frequency of occurrence as well as abundance (cumulative importance value curve), the complete numerical dominance by Emerita and Donax is buffered indicating the significance in terms of diversity, of lesser abundant species.

The large numbers of individuals found concentrated in a few dominant species in this study is typical for environmentally stressed ecosystems (Odum, 1971). Dexter (1969) found a similar deviation (89.5%) of cumulative abundances from maximum diversity on a mesohaline sandy beach at Morehead City, N.C. The concept that naturally stressed areas generally exhibit reduced species diversity is also embodied in Sanders' (1968) stability-time hypothesis. Sanders describes a gradient of marine benthic diversity. At one end he places the "physically controlled community" characterized by adaptations to the physical environment and low diversity. Placed at the other end is a "biologically accommodated community," developed under stable physical conditions over long periods of time and exhibiting high species diversity.

The high energy sandy beach is to a degree the physi-

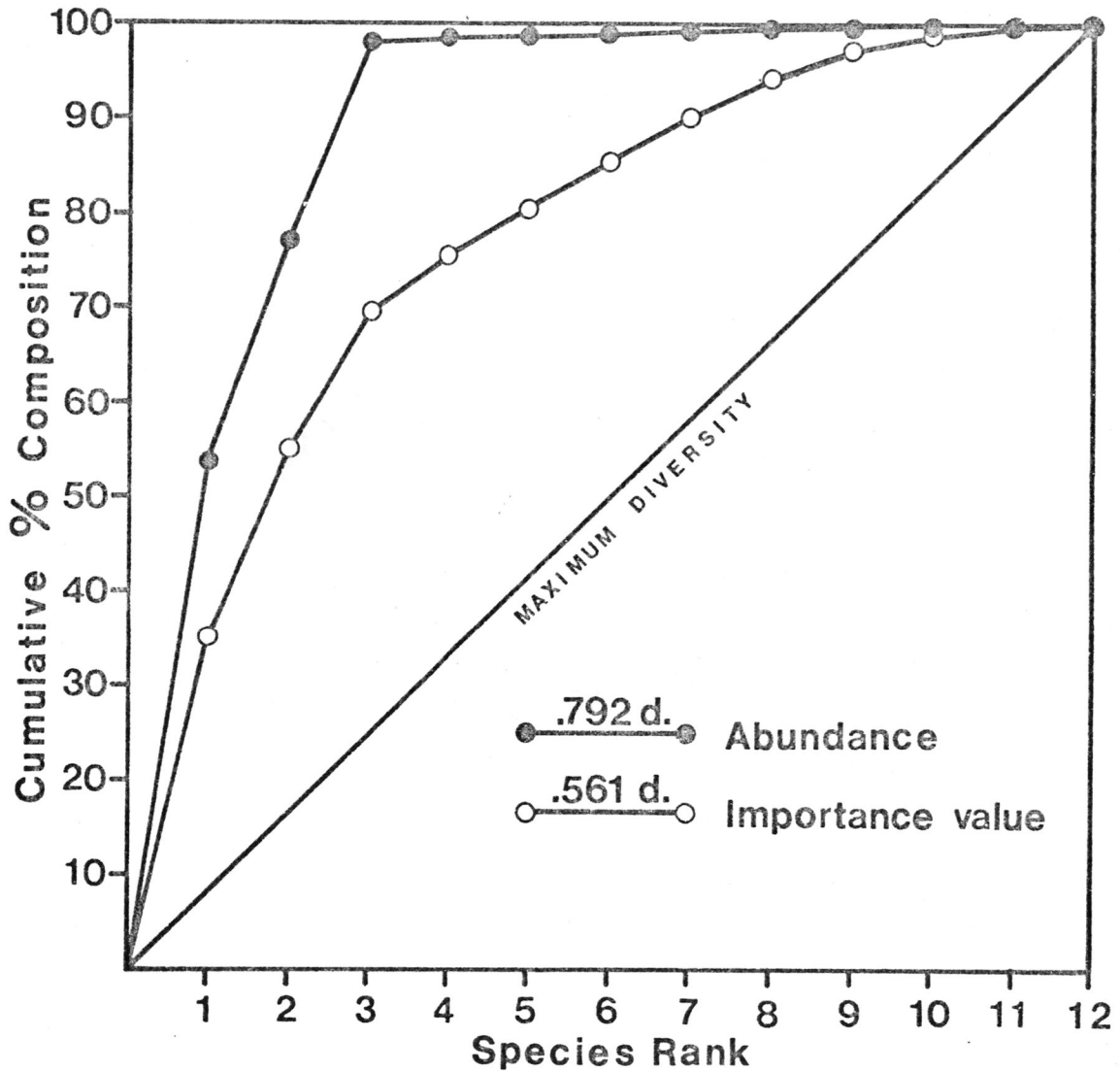


Figure 19. Cumulative percent composition of macrobenthic species ranked by abundance and importance values. The complete numerical dominance by three species is moderated when frequency of occurrence (incorporated within importance values) is considered.

cally controlled community, described by Sanders and characterized by low diversity. It is regulated both by seasonal temperature fluctuations and lack of substrate stability, which presumably arrest community succession in an early stage of development.

That low diversity parameters do not necessarily imply ecosystem instability (Margalef, 1975; May, 1975) is a concept supported by this study. Though not measurable in quantitative terms, the pulse stability apparent on Bogue Banks is supported by efficient species adaptations in morphology, life history, and behavior (as described in this research) to a harsh physical environment; the capacity of primary consumers to generate an extensive standing crop; and the availability of this rich food supply to terrestrial, semi-terrestrial, and strictly aquatic species, i.e., birds, Ocypode, portunids, and fish. This stability is augmented by interactions among these communities within an integrated, composite ecosystem, functioning in phase with changes in its environment. While diversity based on species numbers and richness and determined with mathematical equations is low, there is a diversity of interactions among species and between organism and environment here, which stabilize and bind the aquatic and terrestrial communities. The complexity and diversity inherent through interactions in this ecosystem

is not readily apparent from observations of only a spatial or temporal portion. It should be considered, rather, as an interrelated macrocommunity with emphasis on seasonality and interactions among its component parts.

SUMMARY

1. The sandy beach in this study is physically controlled and characterized by: (1) long term faunal adaptations to temperature and tidal periodicity and a shifting substrate, (2) an Emerita-Donax dominated community structure, and (3) low diversity.

2. Dominant macrobenthic organisms were located in the tidally migrating wash zone and included the mole crab, Emerita talpoida; the coquina clam, Donax variabilis; and the beach clam, Donax parvula. Other species in this ecosystem, in order of relative position on the beach from dry sand to surf, included the beach flea, Talorchestia megalopthalma; the ghost crab, Ocypode albicans; the haustoriid amphipods, Haustorius canadensis and Amphiporeia virginiana; the cirolanid isopod, Chiridotea caeca; the polychaete, Nephtys picta; and the portunid crabs, Arenaeus cribrarius, Ovalipes ocellatus, and Callinectes sapidus.

3. The sandy beach is a composite of overlapping, adjacent communities. There is a strong interdependence among the wash zone community and the adjacent upper beach and nearshore surf zone communities.

4. Trophi-dynamics functionally interrelate these adjacent communities. Littoral POM inputs are utilized

by wash zone primary consumers, especially Emerita and Donax, which effectively convert this energy base into a vast standing crop. This biomass supports several organisms which migrate to the wash zone from adjacent communities to feed. Included here are ghost crabs, portunid crabs, fish, and several species of beach birds.

5. Standing crop estimates indicate the ecosystem is not food limited.

6. Comprehensive studies are needed relating fish and bird densities to primary consumer abundance on the beach.

7. Stability in this ecosystem is augmented by adaptations to the physical environment which enable stratification of species into adjacent habitats during times of stress.

8. There is strong seasonal regulation of abundance and frequency of occurrence of species. Yet, a high degree of pulse stability is evident with the same species repopulating the beach year after year.

9. There is a seasonal succession of numerical dominance.

10. Beach systems should be studied seasonally, especially in temperate zones where dominance of certain species fluctuates.

11. Though mathematical species diversity is low, there is a rich, though presently unquantifiable,

diversity of interactions which enhance stability in this ecosystem.

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